

# Benthic metabolism in San Quintin Bay, Baja California, Mexico

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**ABSTRACT:** Benthic metabolism was measured at 3 representative lagoon bottom sites in San Quintin Bay, Baja California, Mexico, during winter and summer from 1997 to 2000. At each site, and in every sampling period, three 0.5 m diameter transparent acrylic hemispherical domes were installed on bare sediment for ~24 h to determine fluxes of dissolved inorganic carbon (DIC), total alkalinity (TA), dissolved oxygen (O<sub>2</sub>) and dissolved inorganic nutrients (NH<sub>4</sub>, PO<sub>4</sub>). Our results for sediment fluxes (mean ± SE; n = 63), all in mmol m<sup>-2</sup> d<sup>-1</sup>, except TA in meq m<sup>-2</sup> d<sup>-1</sup> were: O<sub>2</sub> = -23.4 (±10.7); DIC = 31.0 (±22.9); TA = 8.1 (±8.0); NH<sub>4</sub> = 2.15 (±1.39); PO<sub>4</sub> = 0.114 (±0.140). These values fall near the median of values reported for shallow water systems. The benthic and planktonic metabolic rates were also compared. Seagrass beds were apparently responsible for ~80% of the benthic metabolism. Benthic processes dominate the metabolism at the system level, accounting for about ~70% of total primary production (PP) and respiration (R). A whole-system production to respiration ratio of ~0.9 was obtained. While recycling dominates gross metabolism, there must be an external supply of organic material to account for an excess of R over PP (net heterotrophy). We conclude that plankton external supplied from outside the system dominates this external supply. Our data agree with previous information for Tomales Bay, California, that deep sediment DIC release was about twice O<sub>2</sub> uptake. These results indicate that anaerobic metabolism accounted for about half the net respiration in the deep sediments.

**KEY WORDS:** Nutrient fluxes · Gross metabolism · Benthic-pelagic coupling · Seagrass · Temperate coastal lagoon

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## INTRODUCTION

In shallow estuaries and lagoons, organic carbon production, sedimentation, and various aerobic and anaerobic respiration pathways (remineralization) link benthos and water column metabolism (Kemp & Boynton 1984, Jørgensen & Sørensen 1985, Rizzo 1990, Dollar et al. 1991, Kemp et al. 1992). Unlike plankton-dominated deep ocean systems, both the benthos and water column figure prominently in both the primary production and the respiration of these shallow systems. Time scales of this coupling tend to be from hours to days (Nixon 1981, Smith & Hollibaugh 1993, 1997, D'Avanzo et al. 1996). A strong linear relation-

ship between the amount of organic matter produced and/or imported and the amount of organic matter consumed on the bottom has been described for coastal marine ecosystems (Hargrave 1973, Nixon 1981, Hopkinson 1985, Smith & Hollibaugh 1993).

By analyzing the magnitude and ratios of benthic nutrient, carbon and oxygen fluxes, it is possible to gain insight into the pathways of carbon, nitrogen and phosphorus cycling, and the factors that control them at a given location (e.g. Nixon 1981, Dollar et al. 1991, Forja et al. 1994, Giblin et al. 1997). When benthic metabolic rates are compared with water column rates, it is possible to assess their individual contribution to total-system carbon and nutrient cycles, both tempo-

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rally and spatially (Nixon & Pilson 1984, Kemp et al. 1997, Smith & Hollibaugh 1997). Despite the relevance of the geochemical and ecological information obtained through 'stoichiometric analysis' of flux ratios, few studies have used it. The approach has seen wider use over the past decade as part of the IGBP-LOICZ project, largely as a way to retrieve information about ecosystem metabolism from secondary data (<http://data.ecology.su.se/MNODE/>).

We were interested in describing benthic metabolism in San Quintin Bay, Baja California, Mexico, a temperate climate marine lagoon system, to answer the following questions: (1) How large is the contribution of benthic metabolism (production and respiration) to ecosystem-level metabolism? (2) Which are the spatial patterns in benthic fluxes between and within habitats? (3) What controls the magnitude and stoichiometric ratios of benthic fluxes? San Quintin Bay is hydrographically and climatically similar to Tomales Bay, California, USA, an extensively studied system approximately 1000 km to the northwest (e.g. Smith & Hollibaugh 1997 and references therein). Therefore, (4) how similar is the biogeochemical functioning of these 2 bays, when analyzed with internally consistent methodology?

Much of the coastal ocean is profoundly impacted by human activities and by climate change and variability. Therefore, a further interest of this site comparison is due to the fact that these 2 systems are both relatively unimpacted (Smith & Hollibaugh 1997, Aguirre-Muñoz et al. 2001). Less information exists on the fate and transport of nutrients in coastal lagoons and bays receiving relatively little terrestrial inputs, than for river-dominated coastal plain estuaries (Boydton et al. 1996, Largier et al. 1997). As development pressure continues in the coastal zone, there is an urgent need to understand ecosystem functioning in less disturbed conditions such as in San Quintin and Tomales Bays.

## MATERIALS AND METHODS

**Study area.** San Quintin Bay is located at 30° 30' N, 116° W, on the Pacific coast of Baja California about 300 km south of the Mexico-USA border (Fig. 1). It covers an area of 42 km<sup>2</sup> and has a mean depth of about 2 m. Tides are semidiurnal with a mean amplitude of 1.6 m (C. Nava, Sea Level Laboratory, CICESE, pers. comm.). The most conspicuous benthic community in the system is the eelgrass (*Zostera marina*) (Ibarra-Obando & Huerta-Tamayo 1987, Poumian-Tapia & Ibarra-Obando 1999). Ward et al. (2003) assessed changes in major habitat coverage between 1987 and 2000. As simplified and generalized from Ward et al.

(2003), marine habitats are represented by exposed and submerged eelgrass, mudflat, channel (deep mud) and salt marsh (Fig. 1).

Whole-system net biogeochemical characteristics have been described by Camacho-Ibar et al. (2003), and characteristics of anthropogenic use of the bay and its interaction with the adjacent land are described by Aguirre-Muñoz et al. (2001).

**Methodology.** Two sets of primary data are presented in this paper. Measuring metabolism of the deep channel sediments was the major thrust of the study. Therefore, procedures for those measurements are detailed below and are the major topic presented in the Results. In addition, we estimated metabolism in the water column. This constitutes a relatively minor portion of the 'Results'.

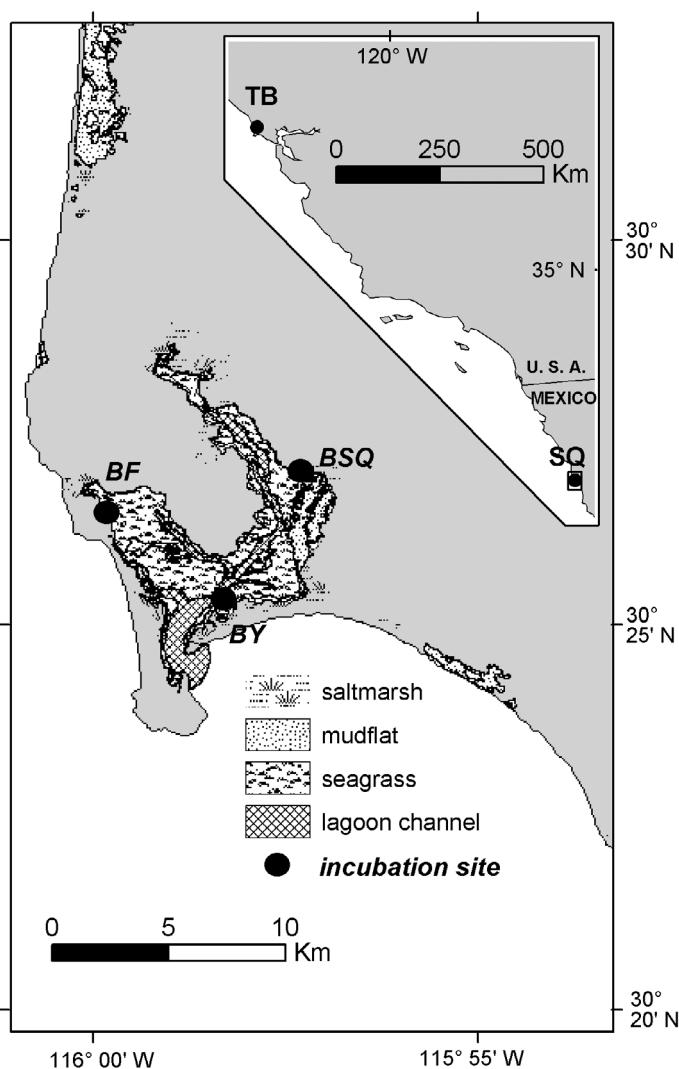


Fig. 1. San Quintin Bay, Baja California (SQ), also showing location of Tomales Bay, California (TB) (inset). The main habitats described in Ward et al. (2003) are shown. Full circles indicate experimental sites

Because we wished to consider other aspects of total system metabolism and to compare our results with other coastal systems, we also undertook a relatively detailed (although hardly comprehensive) literature survey both of San Quintin Bay and of the broader coastal ecological literature. Our database (<http://ecologia.cicese.mx/~sibarra>) on benthic fluxes includes a total of 75 references from shallow (<20 m) and deep (20 to 100 m) coastal sites. This 20 m depth was used as a cut-off between 'shallow' and 'deep' sites, because there was a natural break in the frequency distribution near 20 m, with a scattering of sites at greater depths. The database on benthic-pelagic coupling includes 29 references from 17 sites. For comparative purposes, only those studies in coastal environments, in which fluxes were measured on sediments devoid of macroscopic vegetation, were included. The final data base for benthic fluxes consists of 61 references from 57 locations. In the case of benthic-pelagic coupling, the final database consists of 28 references from 16 locations. We also conducted a literature survey of data on microphytobenthos production from coastal temperate ecosystems, available at the same web page as above. This database contains 32 references for 29 sites.

**Deep sediment fluxes.** Sampling took place each February and August between February 1997 and February 2000. These sampling periods were assumed to capture the winter and summer extremes of the annual cycle, have similar length and provide comparison with the Tomales Bay study (Dollar et al. 1991). In Tomales, whole-system and benthic metabolic rates were represented by an essentially saw-toothed oscillation between winter low values during the January bimonthly sampling and summer high values in August (Smith & Hollibaugh 1997). We therefore estimate annual average values as the averages of the February and August data (properly weighted for 4 February and 3 August sampling periods).

We used the subsystems previously described by Camacho-Ibar et al. (1999, 2003) to choose our 3 sampling locations: Bahia San Quintin (BSQ), Bahia Falsa (BF) and Base of the Y (BY) respectively (Fig. 1). As in Dollar et al. (1991), transparent plexiglas hemispherical domes 50 cm in diameter enclosing a water volume of approximately 33 l were used. On each sampling period, 3 domes were deployed for approximately 24 h in water depths of about 4 m, over sediment devoid of macroscopic vegetation, at each of the 3 locations. The 4 m depth was considered to represent the mean depth of channels.

As we did not have funds for stirrers, the possibility of reduced oxygen concentration at the sediment-water interface of the domes existed. Considering this, and because our preliminary summer data indicated

that after periods much longer than 12 h, oxygen in the domes could be exhausted, it was decided to deploy the domes and then move them about 0.5 m after half-day periods. This procedure allowed complete replacement of the water in the dome, assuring that there would be enough oxygen to complete the 24 h incubation period. This procedure was followed, both in summer and winter, for internal consistency.

Four sets of water samples were withdrawn from each dome at each location during a 1 d incubation:  $t_0$ , a few minutes after installation, allowing for most sediment to settle;  $t_1$ , after the day or night incubation period;  $t_2$ , after moving the domes and allowing time for sediment to settle; and  $t_3$ , after the additional incubation period. Fluxes were estimated for the periods ( $t_1 - t_0$ ) and ( $t_3 - t_2$ ). Water samples were collected into 140 ml plastic syringes withdrawn through a stopcock, while a second stopcock remained open to allow replacement of the sample volume with bay water. Our calculations indicated that the water volume replaced during sampling represented 2% of dome volume. Four syringes were filled per dome at each sampling interval. Syringes were kept < 1 h in an empty Styrofoam ice chest, near ambient temperature, during transport to the laboratory.

Once samples were in the laboratory, dissolved oxygen and temperature were measured directly in the syringes with a YSI 58 digital oxygen meter (nominal precision  $0.01 \text{ mg l}^{-1}$ ); pH was measured in the same syringe with a 290A Orion pH meter (nominal precision 0.002 pH units). The oxygen electrodes were air calibrated at the beginning of each measurement sequence. Water samples for other analyses were filtered through GFC filters. Filters were kept frozen in the dark for chlorophyll *a* determination. About 75 ml of filtered water was held at room temperature for total alkalinity (TA) measurement within the next few days by the method of single-point acid (0.01N HCl) addition, and determination of pH of the acidified sample (Smith & Kinsey 1978). Water samples for dissolved inorganic nutrient measurement ( $\text{NH}_4$ ;  $\text{PO}_4$ ) were filtered into HCl-washed, sample-rinsed polyethylene bottles and kept frozen until analyzed.  $\text{NO}_3$  was not measured, as pilot studies demonstrated the  $\text{NO}_3$  fluxes to be small and inconsistent in direction (see also Dollar et al. 1991, for Tomales). Samples for 1997, 1998 and winter 1999 were analyzed with a Milton Roy Plus Spectronic 1001 spectrophotometer using standard techniques described in Strickland & Parsons (1972). Summer 1999 and winter 2000 samples were analyzed automatically using a segmented flow analysis system (S.F.A.S.) Skalar San Plus (precision  $0.1 \text{ } \mu\text{M}$ ). Chlorophyll *a* was determined using fluorometric techniques as described in Strickland & Parsons (1972).

Benthic fluxes were calculated using the equation given by Dollar et al. (1991):

$$J = V(C_t - C_0)/(AT)$$

where  $J$  = benthic flux per unit area of bay bottom,  $V$  = volume of water enclosed within the incubation chamber over the sediment ( $\sim 0.033 \text{ m}^3$ ),  $C_t$  and  $C_0$  = dissolved concentrations at the end and beginning of each incubation period,  $A$  = area of sediment enclosed ( $\sim 0.20 \text{ m}^2$ ), and  $T$  = time. It is implicit in the equation that positive fluxes release dissolved materials to the water column, while negative fluxes remove dissolved material out of the water column.

An initial comparison was made in the differences between day and night fluxes. Then, fluxes for day and night periods were cumulated in order to derive daily net fluxes. Rates from the 3 chambers were averaged at each site and on each date. Based on previous experience (Smith et al. 1981, Dollar et al. 1991, Smith & Hollibaugh 1997), concentrations in the domes were assumed to vary linearly. Benthic fluxes were not corrected for water column metabolism as the average dome depth is small (<10% of the average water column in the bay; <5% of the depth at the deployment sites). Corrections for water column metabolism would be within the analytical errors of the flux estimates (see below).

**Plankton metabolism. Primary production:** In order to compare benthic and pelagic primary production, phytoplankton primary production was measured during one August and one February period, using the  $^{14}\text{C}$  technique. In order to extend the results, we used an empirical model developed by Montes-Hugo (2001) and Montes-Hugo & Alvarez-Borrego (2003) for San Quintin Bay. The primary difference between this model and the one developed by Cole (1989) for Tomales Bay is that we parameterize primary production as an exponential function of depth at each station ( $\sim 4 \text{ m}$ ) and attenuation coefficient (characteristically  $\sim 0.6 \text{ m}^{-1}$ ; measured several times during summer and winter ebb tides in 1999; see also Cabello-Pasini et al. 2003). Characteristic depths for 50, 10 and 1% light were approximately 1, 4 and 8 m, respectively. Most of the bay is shallower than 4 m.

Surface-water phytoplankton production was measured at the 3 sampling sites during August 1999 and February 2000. At each site, 3 sets of replicates were used. Each set consisted of 2 clear and 1 dark 250 ml polycarbonate bottles inoculated with  $5 \mu\text{Ci } ^{14}\text{C}$ . Bottles were held at 1 m water depth for 2 h (11:00 to 13:00 h). Once in the laboratory, water samples were filtered through a Gelman 0.45  $\mu\text{m}$  filter that was kept in a scintillation vial to which we added 0.5 ml HCl. After about 10 h, 10 ml of a liquid scintillation cocktail (Ecolite) were added to the vial. Filters were read in

a Beckman LSC-100 liquid scintillation counter at Scripps Institution of Oceanography. The amount of  $^{14}\text{C}$  fixed was calculated with the equation given by Strickland & Parsons (1972).

**Respiration:** Each time the domes were deployed, water samples for measurement of plankton respiration were collected from the surface into 20 l carboys. Once in the laboratory, water was siphoned into 3 sets of replicate 300 ml opaque glass BOD bottles, allowing overflow before capping. The bottles were incubated for 36 h in a water bath at field temperature ( $\pm 0.5^\circ\text{C}$ ). Oxygen was measured in 2 replicate bottles from each set, at 12 h intervals over the 36 h (following Fourqurean et al. 1997). The oxygen meter and probe were calibrated at the beginning of each measurement sequence using water-saturated air at the temperature of incubation. The electrode was placed in each bottle and allowed to equilibrate until a constant reading was obtained.

Preliminary analyses demonstrated that respiration in the bottles consumed about  $8 \mu\text{mol O}_2 \text{ l}^{-1}$  over a 12 h period. This is a weak analytical signal. As seawater has typically about  $200 \mu\text{mol O}_2 \text{ l}^{-1}$ , a change of only about 4% would have taken place over 12 h. We, therefore, ran the incubations for 36 h in order to achieve total changes in the 10% range. While we recognize that this could introduce artifacts (slowed or accelerated respiration, largely dependent upon either exhausting the substrate or building up bacterial biomass), we saw no evidence of such rate changes in preliminary studies.

## RESULTS

### Deep sediment fluxes in the incubation chambers

End-point oxygen concentrations measured throughout all incubations ranged between 1.8 and  $12.2 \text{ mg l}^{-1}$ , with a mode of  $7.6 \text{ mg l}^{-1}$  (Fig. 2). Measured fluxes were apparently not compromised by lack of oxygen, as oxygen saturation at the end of incubations was never below 20% and mostly above 60%.

We considered the possibility that there were significant day versus night fluxes in the bay-channel sediments (Table 1). Only the summer DIC fluxes showed a significant day-night difference. Nighttime dissolved inorganic carbon (DIC) fluxes exceed daytime fluxes by  $17 \text{ mmol m}^{-2} \text{ d}^{-1}$ . TA,  $\text{O}_2$  and nutrient fluxes showed insignificant day versus night differences.

Fluxes over complete 24 h cycles for the 3 sites and for the whole bay are presented in Table 2. Further evidence that benthic fluxes were not affected by lack of oxygen comes from the scatterplot of  $\text{O}_2$  flux and

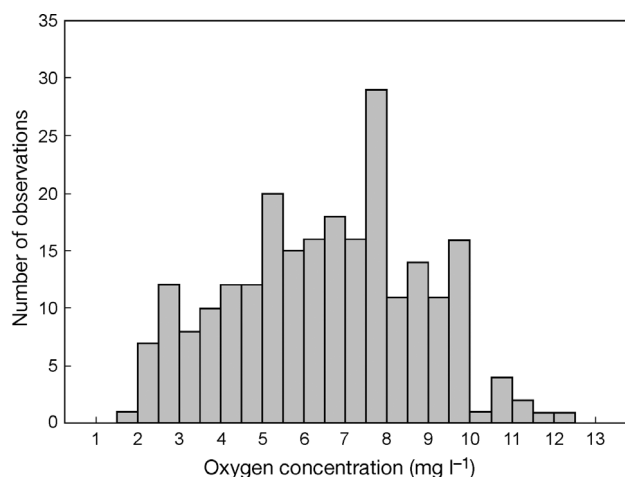


Fig. 2. Histogram showing the frequency of observations at the various oxygen concentrations ( $\text{mg l}^{-1}$ ) at the end of the incubations periods. Most of the values were above  $2 \text{ mg l}^{-1}$

DIC flux, which shows that there was a significant linear relationship between  $\text{O}_2$  consumption and DIC production (slope  $\sim -1.9$ ; intercept near 0), indicating substantial anaerobic respiration, but no change of slope at high DIC production (Fig. 3). As both  $x$  and  $y$  variables are subject to errors, regression model II was applied (Ricker 1973). DIC flux is assumed to represent total organic matter oxidation and consistently exceeds  $\text{O}_2$  flux (except near 0).

Significant differences between sites were found for  $\text{O}_2$ , DIC and  $\text{NH}_4$  fluxes. The stations in the 2 arms (BSQ and BF) are similar to one another and differ from the mouth (BY) (Table 3). BY consistently showed elevated fluxes relative to both BSQ and BF. While the differences may represent spatial trends within regions of the bay, we cannot evaluate an appropriate spatial weighting or even interpret this as anything other than differences between the 3 stations. We, therefore, use

Table 1. Whole-bay comparison between daytime and nighttime fluxes. Values are  $\text{mmol m}^{-2} \text{ d}^{-1}$  except TA, which is  $\text{meq m}^{-2} \text{ d}^{-1}$ . Mean  $\pm 1$  SD (number of samples). \*Day-night pairs significantly different from one another at  $p < 0.05$  (summer DIC only); <sup>a</sup>fluxes differ from 0 at  $p < 0.05$ . Note that 1 set of winter  $\text{NH}_4$  samples was lost and 1 summer value for TA flux was an outlier. DIC: dissolved inorganic carbon; TA: total alkalinity;  $\text{NH}_4$ : dissolved inorganic nitrogen;  $\text{PO}_4$ : dissolved inorganic phosphate

		$\text{O}_2$	DIC	TA	$\text{NH}_4$	$\text{PO}_4$
Winter	Day	$-14.6 \pm 13.7$ (36) <sup>a</sup>	$18.0 \pm 23.0$ (36) <sup>a</sup>	$7.7 \pm 9.6$ (36) <sup>a</sup>	$1.81 \pm 2.01$ (27) <sup>a</sup>	$0.055 \pm 0.111$ (36) <sup>a</sup>
	Night	$-20.3 \pm 11.7$ (36) <sup>a</sup>	$18.8 \pm 29.4$ (36) <sup>a</sup>	$5.1 \pm 6.7$ (36) <sup>a</sup>	$1.61 \pm 0.84$ (27) <sup>a</sup>	$0.032 \pm 0.122$ (36)
Summer	Day	$-24.8 \pm 18.8$ (27)*	$34.2 \pm 25.6$ (26) <sup>a</sup>	$6.8 \pm 12.7$ (26) <sup>a</sup>	$2.50 \pm 1.71$ (27) <sup>a</sup>	$0.175 \pm 0.361$ (27) <sup>a</sup>
	Night	$-33.8 \pm 14.3$ (27)*	$51.0 \pm 33.2$ (27) <sup>a</sup>	$12.8 \pm 14.3$ (27) <sup>a</sup>	$2.67 \pm 1.79$ (27) <sup>a</sup>	$0.193 \pm 0.249$ (27) <sup>a</sup>

Table 2. Benthic fluxes (mean  $\pm 1$  SD) in San Quintin Bay for the period February 1997 to February 2000. Values are  $\text{mmol m}^{-2} \text{ d}^{-1}$  except TA, which is  $\text{meq m}^{-2} \text{ d}^{-1}$ . It is assumed that winters and summers are reflected by February and August data, respectively; that the annual average conditions are approximately an average of these 2 mo; and that the whole-bay average is represented by the 3 sites. Same abbreviations as Table 1

	$\text{O}_2$	DIC	TA	$\text{NH}_4$	$\text{PO}_4$
<b>Bahia San Quintin (BSQ)</b>					
Winter	$-19.3 \pm 7.5$	$5.0 \pm 16.8$	$3.9 \pm 5.2$	$1.50 \pm 1.57$	$0.047 \pm 0.084$
Summer	$-22.3 \pm 7.9$	$31.5 \pm 12.6$	$9.5 \pm 6.2$	$2.09 \pm 1.03$	$0.177 \pm 0.135$
Annual	$-20.8 \pm 7.7$	$18.2 \pm 14.7$	$6.7 \pm 5.7$	$1.79 \pm 1.30$	$0.112 \pm 0.110$
<b>Bahia Falsa (BF)</b>					
Winter	$-12.4 \pm 4.9$	$17.4 \pm 19.2$	$5.9 \pm 7.4$	$1.03 \pm 0.46$	$-0.005 \pm 0.047$
Summer	$-23.3 \pm 4.7$	$28.2 \pm 21.7$	$10.7 \pm 15.0$	$2.34 \pm 1.50$	$0.167 \pm 0.245$
Annual	$-17.8 \pm 4.8$	$22.8 \pm 20.4$	$8.3 \pm 11.2$	$1.69 \pm 0.98$	$0.081 \pm 0.146$
<b>Base of the Y (BY)</b>					
Winter	$-20.6 \pm 8.3$	$35.4 \pm 14.0$	$9.6 \pm 4.9$	$2.60 \pm 1.19$	$0.088 \pm 0.057$
Summer	$-42.4 \pm 15.5$	$68.4 \pm 17.3$	$9.3 \pm 6.7$	$3.33 \pm 1.64$	$0.209 \pm 0.251$
Annual	$-31.5 \pm 11.9$	$51.9 \pm 15.6$	$9.4 \pm 5.8$	$2.96 \pm 1.42$	$0.148 \pm 0.154$
<b>Whole Bay</b>					
Winter	$-17.4 \pm 7.7$	$19.3 \pm 20.7$	$6.4 \pm 6.2$	$1.71 \pm 1.30$	$0.043 \pm 0.074$
Summer	$-29.3 \pm 13.7$	$42.7 \pm 25.1$	$9.8 \pm 9.8$	$2.59 \pm 1.47$	$0.184 \pm 0.205$
Annual	$-23.4 \pm 10.7$	$31.0 \pm 22.9$	$8.1 \pm 8.0$	$2.15 \pm 1.39$	$0.114 \pm 0.140$

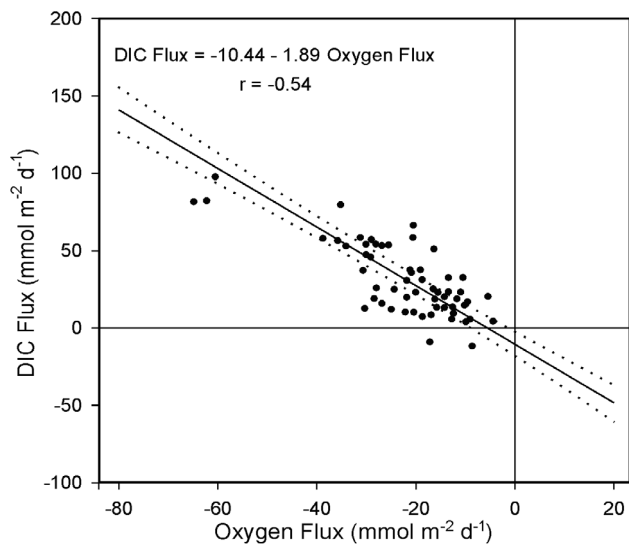


Fig. 3. Scatter diagram of benthic oxygen flux versus DIC flux. Dotted lines represent the 95% confidence interval

a simple average of the 3 stations as an estimate of whole-bay channel sediment metabolism.

DIC and  $O_2$  flux are significantly correlated ( $r = -0.54$ ), with a DIC/ $O_2$  flux ratio of about  $-1.9$  determined from the regression slope. This suggests that about half of the net sediment respiration is anaerobic. We recognize that gross respiration in the sediments is likely to be more strongly anaerobic (dominated by sulfate reduction), with subsequent oxidation of sulfide not bound into minerals back to sulfate (see discussion in Smith & Hollibaugh 1997). Regression analyses of benthic nutrient fluxes show significant, although low, correlation coefficients (Fig. 4). The slopes of regression equations gave the following ratios: the ratio of dissolved inorganic nitrogen to dissolved inorganic phosphate (DIN/DIP) regression slope of  $8 \pm 1$  is not significantly different from Redfield N/P (16) ( $p > 0.05$ ) (Redfield 1958), because of the low correlation. The slope for DIC/DIN is  $20 \pm 2$ , about 3 times the Redfield N/P value of 6.6. The slope for DIC/DIP is 136, or about 30% above the Redfield value of 106. Both the C/N and C/P slopes differ from Redfield ( $p < 0.01$ ). We believe that the slopes, rather than the average flux ratios, are the

Table 3. Probability values of the 1-tailed *t*-test for benthic flux differences between stations. Probabilities  $< 0.05$  are statistically significant. Same abbreviations as Table 1

Sites	$O_2$	DIC	TA	$NH_4$	$PO_4$
BSQ–BF	0.130	0.366	0.565	0.806	0.478
BF–BY	$< 0.001$	$< 0.001$	0.578	0.008	0.202
BSQ–BY	0.021	$< 0.001$	0.090	0.016	0.436

appropriate metric for comparison with Redfield, because of the clear evidence for DIP sorption. We assume this sorption to be approximately constant and of decreasing importance as the fluxes increase. This process accounts for the significant negative DIP intercepts on Fig. 4. Using Redfield ratios as a reference, benthic N flux was about 50% below expectation based on P and 65% below expectation based on C. This suggests a sink for regenerated N with respect to regenerated C and P. We interpret this sink to be denitrification.

If the reactants leading to the DIP and DIC fluxes are a mixture of plankton (C/P  $\sim 106$ ) (Redfield 1958) and seagrass (C/P  $\sim 550$ ) (Atkinson & Smith 1983), it can be demonstrated from the DIC/DIP flux slope (136) that plankton dominates the reacting organic matter.

### Water column metabolism

Midday 1 m  $^{14}C$  primary production (PP) averaged  $19 \pm 2 \text{ mg m}^{-3} \text{ h}^{-1}$  (mean  $\pm$  SE) for the 3 sampling sites during August 1999 and  $8 \pm 1$  during February 2000. The mean hourly production/chlorophyll assimilation number for these data was 8.7. A second data set by Montes-Hugo (2001; also Montes-Hugo & Alvarez-Borrego 2003) gave a mean assimilation number of 7.0, so we use a mean assimilation number of 8 for phytoplankton in San Quintin Bay. We apply this value, an extinction coefficient of  $0.6 \text{ m}^{-1}$ , and mean summer and winter solar radiation values of 2100 and 1500  $\mu\text{mol quanta m}^{-2} \text{ s}^{-1}$  to median summer and winter chlorophyll concentrations throughout this study (4.6 and 1.7  $\text{mg m}^{-3}$ , respectively) to calculate PP for the 2 m water column: 68  $\text{mmol C m}^{-2} \text{ d}^{-1}$  (summer) and 25 (winter), for an average of 47  $\text{mmol m}^{-2} \text{ d}^{-1}$ .

Water column respiration (R) over the period of the study averaged  $28 \pm 3 \text{ mmol m}^{-3} \text{ d}^{-1}$  (mean  $\pm$  SE) during the summer and  $25 \pm 2$  during the winter. These rates do not differ, so we use an average rate for the 2 m water column of 53  $\text{mmol m}^{-2} \text{ d}^{-1}$ .

PP and R rates in the water column are apparently 47 and 53  $\text{mmol m}^{-2} \text{ d}^{-1}$ , respectively. While R apparently slightly exceeds PP, uncertainties in the spatial and temporal distribution of 'independent' variables across the bay, as well as differing analytical methodologies preclude any ability to distinguish between PP and R. We therefore use a value of 50, as the best whole-bay estimate of water column PP and R.

### DISCUSSION

With the exception of phosphate and total alkalinity, higher benthic fluxes appear to occur at BY than at either of the other stations (Tables 2 & 3). This result is

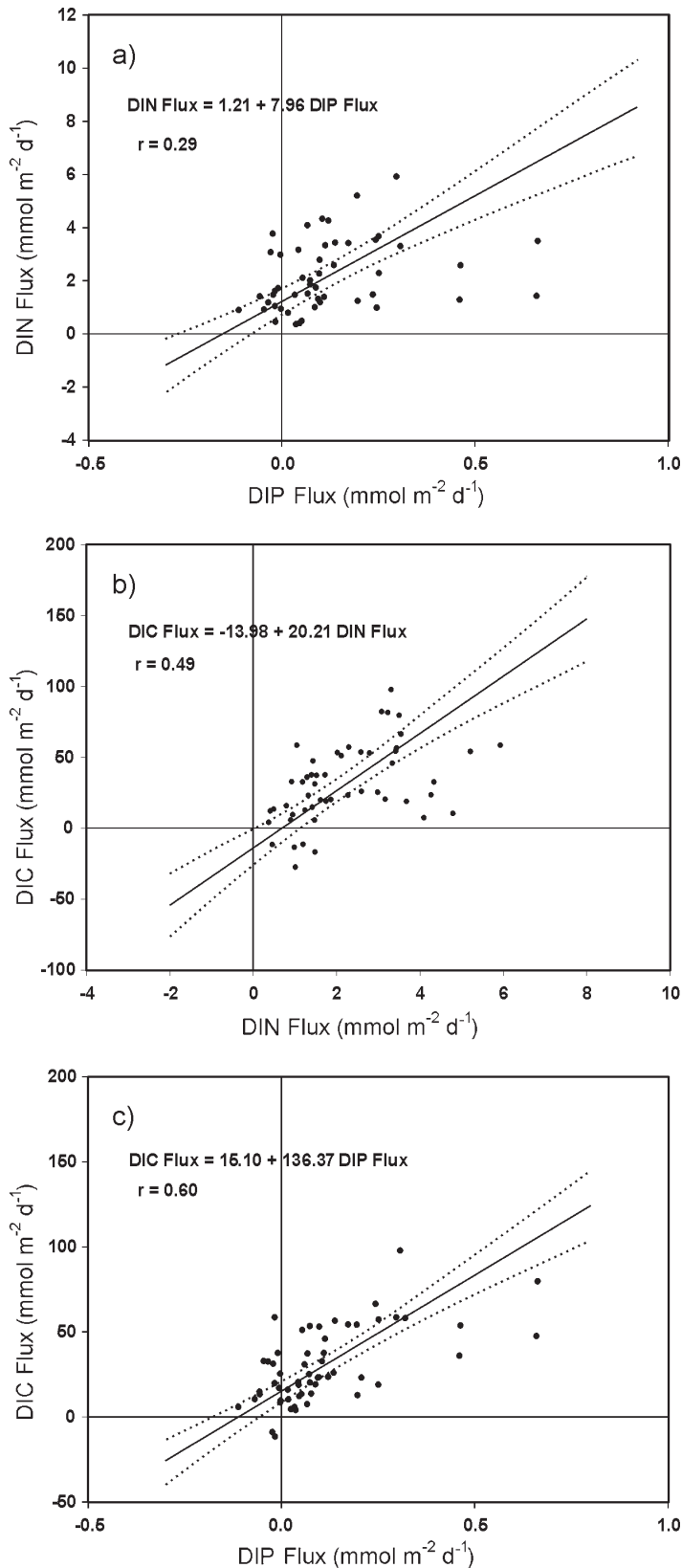


Fig. 4. Regression analysis of benthic fluxes. Dotted lines represent the 95% confidence interval

consistent with the inference of Camacho-Ibar et al. (2003) that marine organic matter is entering the system and much of it is respired near the mouth. However, 3 stations are insufficient to ascertain whether this is truly a spatial pattern or simply variation among these 3 stations. From the C/P flux ratio determined from the regression slope, we conclude that the major source of organic matter on the bottom is planktonic, rather than seagrass detritus. Within the resolution of the data for water column and deep sediment metabolism and our assumptions about fluxes in the other habitats, the only compartment that apparently has  $(\text{PP} - \text{R}) \neq 0$  in this system is the deep sediment community.

### Gross and net metabolism for bay habitats

Following the information laid out in 'Study area' description, we consider the following major habitats in the bay (proceeding from the shoreline to the bay bottom): salt marsh, shallow mud flats, seagrass and lagoon bottom muds. In addition, the planktonic community occurs throughout the bay. In this section, we reconcile our data and literature data on primary production and respiration within each habitat, in order to derive baywide 'best estimates' of gross and net metabolism.

#### Plankton

While more detailed analysis of the water column metabolism might suggest variations throughout the system, we conclude that water column PP and R are more or less homogeneous throughout the system and approximately equal ( $\text{PP} \approx \text{R} \approx 50 \text{ mmol m}^{-2} \text{ d}^{-1}$ ).

#### Salt marsh

There is a fringe of salt marsh vegetation on much of the coastline of the bay (Fig. 1). While we did not directly measure the salt marsh productivity, we provide estimates for habitat comparisons. From Ward et al. (2003), we estimate that this fringe occupies about 20% of the bay area. Zedler (1980) has studied PP of rather similar salt marshes in Tijuana Estuary, 300 km to the northwest of San Quintin. She estimated these marshes to have a PP of approximately  $80 \text{ mmol C m}^{-2} \text{ d}^{-1}$ ; we use this value for San Quintin. Obvious salt marsh detritus is not found much removed from the habitat itself and there is no evidence of much organic matter accretion in these marshes. We therefore assume that PP largely decomposes in place. Thus R is also estimated at

80 mmol m<sup>-2</sup> d<sup>-1</sup>. These values for PP and R within the salt marsh habitat can be prorated to give estimates of the salt marsh to bay-wide PP and R: 16 mmol m<sup>-2</sup> d<sup>-1</sup> (Table 4).

#### Shallow mud flats

We have also not analyzed the metabolism of the shallow mud flats, which also occupy about 20% of the bay area. We have considered this metabolism from 2 general approaches. (1) We consider the growing base of literature on the PP of microphytobenthos populating estuarine mud flats. (2) We consider some model results which we thought were a promising tool. It can be seen in Fig. 5 that, while there is a wide range in estimated rates of PP in these environments, there is a strong mode between 30 and 100 mmol m<sup>-2</sup> d<sup>-1</sup> and a median value of about 20 (<http://ecologia.cicese.mx/~sibarra>). These data include both intertidal and subtidal sites, with no significant difference in the median.

The second approach we considered was to model the microphytobenthos productivity from sediment chlorophyll (average ~70 mg m<sup>-2</sup>; Ibarra-Obando & Elguea-Cazares 1987—note that in this reference, the chlorophyll units in the text are wrong; units from the figures should be used). Available light and light extinction data are discussed above, for the plankton PP. The model we employed is adapted from Webster et al. (2002) for microphytobenthos and is structurally similar to the model employed for the plankton. This model gives a PP in excess of 300 mmol m<sup>-2</sup> d<sup>-1</sup> for benthic microalgae living in a mean water depth of 1 m. While we believe that such a model has promise, we are skeptical of the results. This value is above any of the values available in the literature, even though the chlorophyll content of the sediment is apparently reasonable. Further, it seems unlikely that this habitat

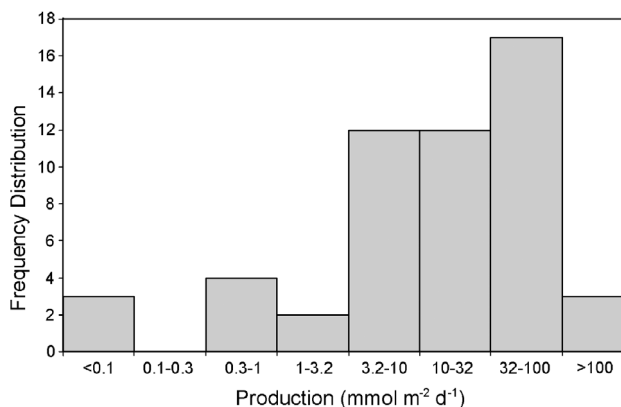


Fig. 5. Frequency distribution of microphytobenthos primary production (PP) (mmol m<sup>-2</sup> d<sup>-1</sup>). Data were obtained from the literature and can be found at <http://ecologia.cicese.mx/~sibarra>

would have a productivity higher than the high-biomass seagrass habitat. Finally, we note that 2 of the 3 highest values for microphytobenthos PP illustrated in Fig. 5 were derived by Webster et al. (2002) from their model.

We suspect that there may be significant problems with assessing the light actually available for the algal community living in the sediment. We will return to this point below, when discussing the lagoon bottom sediment metabolism. In the end, we conclude that the best estimate of mud flat microphytobenthos PP is the median value cited above (20 mmol m<sup>-2</sup> d<sup>-1</sup>). We further assume that any of these production products that become re-suspended would be trapped (filtered) by the adjacent seagrass and are unlikely to move far from the production sites. As argued for the salt marsh, the lack of rapid sediment organic C accumulation argues that PP and R would be similar. Prorated to a bay wide rate, mud flat PP and R are each estimated to be about 4 mmol m<sup>-2</sup> d<sup>-1</sup> (Table 4).

Table 4. Contribution of benthic and water column processes to total system metabolism. Whole bay data for the period August 1998 to February 2000 were used. Primary production (PP) and respiration (R) per unit area of cover for each habitat were multiplied by habitat proportion cover to derive bay-wide rates (mmol C m<sup>-2</sup> d<sup>-1</sup>)

Habitat	Rate within habitat			% of area covered	Bay-wide rate		
	PP	R	(PP - R)		PP	R	(PP - R)
Salt marsh	80	80	0	20 <sup>a</sup>	16	16	0
Shallow sediment	20	20	0	20 <sup>a</sup>	4	4	0
Seagrass	230	230	0	40 <sup>a</sup>	92	92	0
Deep sediment	~10	40	-30	20 <sup>a</sup>	2	8	-6
<b>Total benthos</b>				<b>100</b>	<b>114</b>	<b>120</b>	<b>-6</b>
<b>Water column</b>	<b>50</b>	<b>50</b>	<b>0</b>	<b>100</b>	<b>50</b>	<b>50</b>	<b>0</b>
<b>BAY TOTAL</b>					<b>164</b>	<b>170</b>	<b>-6</b>

<sup>a</sup>Rounded from Ward et al. (2003)

#### Seagrass

Marine macrophytic vegetation is the structurally dominant habitat in San Quintin Bay, covering approximately 40% of the bay area (Ward et al. 2003). The marine vegetation of San Quintin Bay consists mainly of eelgrass *Zostera marina* best developed in the middle parts of the bay on flats that are covered by 0.3 to 0.9 m of water at the lowest tide. Ibarra-Obando & Huerta-Tamayo (1987) reported a range for eelgrass PP between 60 and 410 mmol C m<sup>-2</sup> d<sup>-1</sup>. The mean was about 230 mmol C m<sup>-2</sup> d<sup>-1</sup> in



the seagrass area; weighted across the entire bay, this is equivalent to about  $92 \text{ mmol C m}^{-2} \text{ d}^{-1}$ . Some, but relatively little, seagrass detritus is found on the bay floor, so we again assume that most of the R occurs more or less *in situ*. This observation is consistent with the conclusion (above) that most sediment R is apparently detrital material.

#### Lagoon bottom sediments

Finally we come to lagoon bottom metabolism, the focus of this investigation. From Table 2, we conclude that metabolism on the lagoon bottom averages approximately  $+30 \text{ mmol m}^{-2} \text{ d}^{-1}$ , based on the DIC flux data. This represents net metabolism based on 24 h incubations. From Table 1, day versus night DIC flux data (summer + winter), we estimate that daytime flux is about  $10 \text{ mmol m}^{-2} \text{ d}^{-1}$  slower than nighttime flux, implying that microphytobenthos PP on the bay floor is about this value. The  $\text{O}_2$  flux difference between the day and night is not statistically significant but gives an average difference similar to the DIC flux data. It follows that gross R is about  $40 \text{ mmol m}^{-2} \text{ d}^{-1}$ . These observations can be compared with the microphytobenthos PP model discussed above. The same model gives PP estimates in excess of  $200 \text{ mmol m}^{-2} \text{ d}^{-1}$  for the channel floor, again apparently too high for the reasons previously discussed and also inconsistent with the observed fluxes in the incubation chambers.

The deep lagoon channel sediments occupy about 20% of the bay area, so the baywide levels of PP and R are estimated to be 2 and  $8 \text{ mmol m}^{-2} \text{ d}^{-1}$ , respectively (Table 4). It is worth noting that, unlike the other habitats, we estimate the net metabolism for the lagoon floor clearly differs from 0. Within both our ability to distinguish and our judgment, we assign all of the net metabolic signal of this system to the deep channel sediments.

#### Whole-bay gross and net metabolism

Measurement or estimation of the components of gross metabolism in San Quintin Bay allows us to assess the relative importance of benthic and water column metabolic pathways. As Kemp et al. (1997) concluded, partitioning of overall rates among individual processes allows the description of temporal and spatial patterns. Preliminary estimates of gross metabolism for San Quintin Bay were performed by Smith & Ibarra-Obando (1997) and Camacho-Ibar et al. (2003). We also compared San Quintin gross metabolism with Tomales Bay, determined by Smith & Hollibaugh (1997) with very similar methodologies. It can be seen that in all cases, (PP – R) has values close to zero, hence that PP/R is within about 10% of 1 (Table 5).

Smith & Hollibaugh (1993) noted that, for most ecosystems, PP and R are within 10–20% of one another. As a consequence of both statistical uncertainties and methodological differences between measurements for the various components of total system metabolism, it becomes difficult to quantify NEP (Net Ecosystem Production) by ‘adding the parts’ (Smith & Hollibaugh 1993, 1997). Indeed, when we compare net ecosystem metabolism obtained by summation of the parts (Table 4), with net metabolism at the ecosystem level obtained through the use of nutrient budgets (Camacho-Ibar et al. 2003), our estimate of net heterotrophy represents an apparent underestimate (Table 5). For San Quintin Bay, both adding the parts and direct, whole-system estimates of net metabolism yield  $\text{NEP} < 0$  (net heterotrophy). Tomales Bay seems to have  $\text{NEP} > 0$  when the parts are added, but a negative value with the direct whole-system net estimates (Table 5). We believe (as did Smith & Hollibaugh 1993, 1997) that the discrepancy reflects a propagation of uncertainties when the component fluxes are summed, and that adding the component fluxes rarely can give a reliable estimate of NEP.

Table 5. Comparison of gross and net metabolism between San Quintin Bay, Baja California, Mexico and Tomales Bay, California, USA, expressed in  $\text{mmol C m}^{-2} \text{ d}^{-1}$ . The ‘summed gross’ method adds up primary production (PP) and respiration (R) for major habitats, while the ‘system net’ method uses the hydrographically calculated DIP budget normalized to carbon as an estimate of (PP – R). The ‘combination method’ reports the average of gross PP and R as PP, system net as (PP – R) and calculates R by difference. The combination values shown in bold type are considered to be the best estimates for San Quintin and Tomales Bays, respectively

Location	Method	PP	R	(PP – R)	PP/R	Source
San Quintin Bay	Summed gross	199	209	–10	0.95	Smith & Ibarra-Obando (1997)
	Net and combination	185	200	–14	0.93	Camacho-Ibar et al. (2003)
	Summed gross	164	170	–6	0.96	This study
	<b>Combination</b>	<b>~167</b>	<b>~181</b>	<b>–14</b>	<b>~0.92</b>	<b>Gross from this study, Camacho-Ibar (2003)</b>
Tomales Bay	Summed gross	110	105	+ 5	1.05	Smith & Hollibaugh (1997)
	System net			–12		Smith & Hollibaugh (1997)
	<b>Combination</b>	<b>~101</b>	<b>~113</b>	<b>–12</b>	<b>~0.89</b>	<b>Smith &amp; Hollibaugh (1997)</b>

For both Tomales and San Quintin bays, we have combined an 'average estimate' of PP and R, with a system-level estimate of NEP to derive a 'best estimate' of PP, R, (PP – R) and PP/R (Table 5).

Our values for benthic O<sub>2</sub> and particularly DIC fluxes in San Quintin Bay are highest at Station BY (Tables 2 & 3). This result is consistent with the pattern of net metabolism reported by Camacho-Ibar et al. (2003), who calculated the highest rates,  $-45 \text{ mmol C m}^{-2} \text{ d}^{-1}$ , near the mouth (station BY) during summer. They considered the possibility that higher community R at this site could be responsible for this condition. Heterotrophy is now recognized as a common trend in coastal lagoons and estuaries (e.g. Smith & Hollibaugh 1993, Frankignoulle et al. 1998), with the timing of heterotrophy through the year providing clues to the sources of organic matter that sustains metabolic activity (Hopkinson 1985).

Although not statistically significant, phosphate flux in our study seems to follow the same spatial trend reported by Camacho-Ibar et al. (2003), with higher values at the base of the Y (BY). Anomalously low N/P flux ratios, relative to organic matter composition, have been reported for virtually all coastal waters (Nixon 1981). The interpretation placed on this ratio (Nixon 1981, Dollar et al. 1991 and related studies of Tomales Bay) has been that the 'missing N' has been lost to denitrification. While this may break down in the winter, when fluxes are low and sorption may be of importance to the phosphorus flux (Joye et al. 1996), this latter effect seems to be small when integrated over an annual cycle (Smith & Hollibaugh 1997). Stoichiometric calculations based on the median and mean DIP and DIN fluxes are shown in Fig. 6b, and suggest that 40 to 60 % of the DIN release during oxidation in shallow marine sediments is lost to denitrification. These results are comparable to estimates based on denitrification assays (e.g. Seitzinger 1988).

#### Benthic fluxes in comparison to literature data

For each flux examined, San Quintin falls near the median of values reported for other systems. Nothing suggests the benthic metabolism for this system to differ from most shallow benthic systems (Fig. 6). The fact that NO<sub>3</sub> fluxes were not measured at San Quintin is not a major issue in this analysis, as NH<sub>4</sub><sup>+</sup> is generally the dominant form of dissolved nitrogen flux in shallow ecosystems (compare Fig. 6b & 6c).

#### Benthic-pelagic coupling

Benthic and planktonic metabolism were compared during this study (Table 4). It can be noted that benthic processes dominate the metabolism at the system

level. Among the benthic components and within the limits of our assumptions, seagrass beds are responsible for about 70 % of the PP and R in the bay. Using the baywide PP and R values in Table 5, we obtain an ecosystem PP/R ratio of about 0.9. About 10% of the organic matter respired in this system apparently comes from outside the system. Vertical fluxes from the water column to the deep bay sediments couple organic carbon, nitrogen and phosphorus fluxes, to balance the excess benthic R over PP (Smith et al. 1981).

Nixon (1981) analyzed the benthic-pelagic coupling in diverse estuarine systems, converting the reported oxygen uptake measurements to carbon, by using an RQ of 1. He concluded that benthic R represented about 24 % of the amount of organic matter fixed plus that imported. Dollar et al. (1991) did a similar analysis and added 9 more sites, including Tomales Bay, and they arrived at a rather different conclusion: Tomales Bay sediments respired about 25 % of PP based on DIC flux, close to Nixon's general prediction based on O<sub>2</sub>. However, the sediment O<sub>2</sub> flux in Tomales only accounted for about 15 % of the PP. Almost half of the sediment metabolism apparently was anaerobic respiration that did not subsequently back-react with O<sub>2</sub>. We updated this analysis with a larger database using the following criteria to exclude references: (1) sites deeper than 20 m, (2) laboratory experiments, (3) sites with obviously high organic load other than from PP and (4) sites with salinities well below 10 psu. We end up with 21 data points including Tomales Bay and San Quintin Bay. For these 2 locations and South San Francisco Bay, we also have DIC values (Fig. 7). With the 21 data points we had  $r^2 = 0.38$ . If we consider point #13 as an outlier,  $r^2$  becomes 0.60. As this change has no statistical significance in the slope or intercept, we decided to leave it in and report the regression as  $y = 0.4x + 4$ .

As shown in Figs. 3 & 7, the discrepancy between R expressed in terms of O<sub>2</sub> and DIC, reported by Dollar et al. (1991) for Tomales Bay, can also be seen for San Quintin Bay. With this revised data set, we found that benthic R calculated from O<sub>2</sub> flux represents 40% of PP, a larger percentage than the one reported by Nixon (1981) (Fig. 7). More importantly, it is clear that both for Tomales and for San Quintin, DIC-based estimates of R are about twice the O<sub>2</sub>-based estimates.

South San Francisco Bay appears to differ from these 2 cases; there, DIC fluxes are slightly smaller than O<sub>2</sub> values (Fig. 7). If a correction of about 50 % could be applied to all the data in Fig. 7, the slope of the line would approach 0.8. While data from only 2 sites is insufficient to apply the suggested correction quantitatively, it is qualitatively persuasive evidence that benthic R is likely to dominate total system R in many such shallow marine systems. In another example, Forja et al. (1994) reported that sediments in Cadiz Bay in

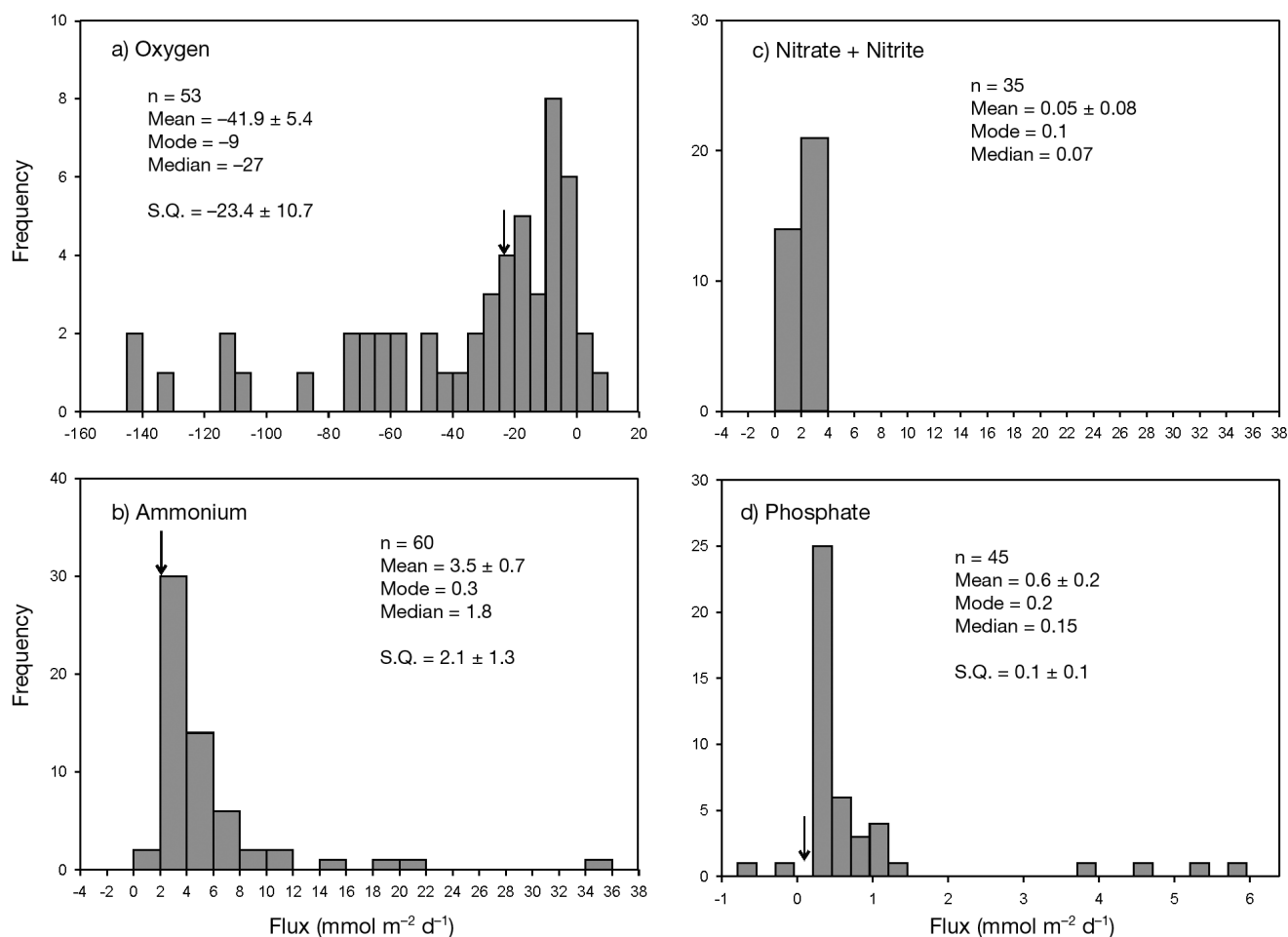


Fig. 6. Histograms showing mean benthic fluxes in shallow marine environments. Values for San Quintin Bay (S.Q. = San Quintin Bay) are indicated with an arrow. (a) Oxygen fluxes; (b) ammonium fluxes; (c) nitrate fluxes. We do not have flux value for S.Q. Bay, but it is likely to be low with respect to  $\text{NH}_4$  flux; (d) Phosphate fluxes. The data base can be found at <http://ecologia.cicese.mx/~sibarra>

Spain have much higher alkalinity flux than  $\text{O}_2$  flux. This study was excluded from the plot in Fig. 7, because the system apparently receives heavy loading from sewage organic matter. While the data cannot be directly converted to DIC fluxes, the high values for alkalinity flux imply that DIC flux substantially exceeds  $\text{O}_2$  flux.

### Comparison between San Quintin and Tomales Bays

San Quintin Bay and Tomales Bay are under rather similar hydrographic and weather regimes due to the presence of upwelling and classical Mediterranean climate (cool, wet winters; hot, dry summers) (Smith & Hollibaugh 1997, Aguirre-Muñoz et al. 2001). The primary difference is the absence of runoff into San Quintin compared to low, but significant, runoff into Tomales. Both systems are light-limited because of high turbidity and both have plankton as impor-

tant primary producers (Lara-Lara & Alvarez-Borrego 1975, Cole 1989, Cabello-Pasini et al. 2003). They also have prominent seagrass (*Zostera marina*) beds (Spratt 1989, Poumian-Tapia & Ibarra-Obando 1999) and a rather similar benthic fauna (Johnson 1970, Sinicrope-Talley et al. 2000).

Both sites are important for mollusk aquaculture (mainly oyster). The human modification of the overall San Quintin catchment has been small, in terms of impacts on San Quintin Bay, although the lower part of the catchment has been intensively cultivated (Aguirre-Muñoz et al. 2001). Because rainfall is low (average =  $150 \text{ mm yr}^{-1}$ ), there is no runoff during most years, and agricultural and domestic sewage discharges do not reach the bay. For Tomales Bay, a similar low level of watershed modification exists, although a major difference is the higher precipitation rate,  $950 \text{ mm yr}^{-1}$ , with an average runoff, normalized to the bay area, of  $300 \text{ mm d}^{-1}$  (Smith & Hollibaugh 1997). Human population density is low in both areas:

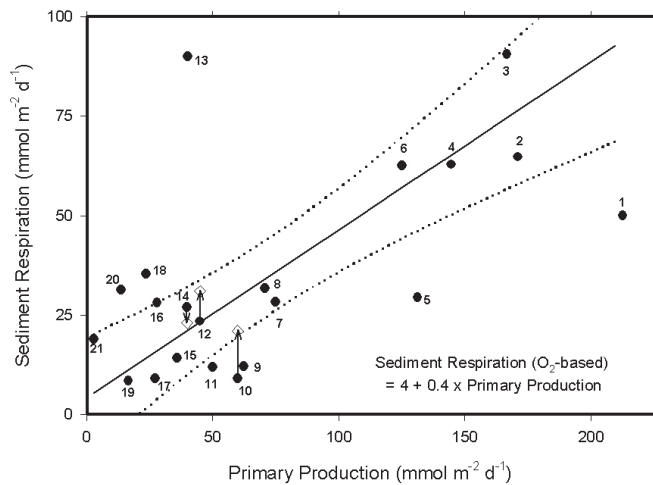


Fig. 7. Scatter diagram of pelagic water column primary productivity (PP) versus sediment respiration (R) in coastal environments (<20 m deep). All sediment R values are expressed as O<sub>2</sub> fluxes (black symbols), except for the 3 explicitly identified as DIC fluxes (empty symbols) for San Quintin Bay, Tomales Bay and South San Francisco Bay. Sources and sites: (1) Kemp & Boynton (1980), Calvert Cliffs, Chesapeake Bay, Maryland, USA; (2) Hopkinson (1985), Georgia Bight, Georgia, USA; (3) Hopkinson & Wetzel (1982); Thomas (1966), Sapelo Island, Georgia, USA; (4) Boynton & Kemp (1985), Chesapeake Bay, Maryland, USA; (5) Kemp et al. (1992), Chesapeake Bay, Maryland, USA; (6) Boynton et al. (1980), Patuxent Estuary, Maryland, USA; (7) Hartwig (1978); Eppley et al. (1970); La Jolla, California, USA; (8) Furnas et al. (1976); Nixon et al. (1976), Narragansett Bay, Rhode Island, USA; (9) Pollehne (1986); Bodungen (1975), Kiel Bight, Germany; (10) Dollar et al. (1991), Tomales Bay, California, USA; (11) Bulleid (1984); Cuff et al. (1983), Port Hacking Estuary, Australia; (12) This study, San Quintin Bay, Baja California, Mexico; (13) Flint & Kamykoski (1984), Port Aransas, Texas, USA; (14) Hammond et al. (1985); Cloern et al. (1985), South San Francisco Bay, California, USA; (15) Smith et al. (1981), Kaneohe Bay, Hawaiian Is. USA, post diversion conditions; (16) Seitzinger (1987); Myers & Iverson (1981), Ochlockonee Bay, Florida, USA; (17) Nowicki & Nixon (1985 a, 1985b), Potter Pond lagoon, Rhode Island, USA; (18) Florek & Rowe (1983), New York Bight, Massachusetts, USA; (19) Smith et al. (1981), Kaneohe Bay, Hawaiian Is., USA, pre diversion conditions; (20) Rizzo (1990), York River, Gloucester Point, Virginia USA; (21) Knoppers et al. (1996), Ararama lagoon, Brazil. Dotted lines are 95% confidence interval

~20 persons km<sup>-2</sup> in the catchment of Tomales Bay (Smith & Hollibaugh 1997) and 13 persons km<sup>-2</sup> in San Quintin Valley (Aguirre-Muñoz et al. 2001).

When compared with similar methodology, it becomes evident that the metabolic performance of the 2 systems is rather similar. Our study exemplifies how a regional perspective can be developed, when sites are compared using the same methodology. This regional perspective is necessary in order to characterize the relationship of nutrient fluxes to environmental change, including human intervention (Holligan & Reiners 1992).

## Summary

The analysis of benthic fluxes indicated that in San Quintin Bay, about half of sediment respiration is anaerobic and that the major source of organic matter respired on the lagoon floor is planktonic, rather than seagrass detritus. Values for benthic fluxes in San Quintin are similar to those described for most shallow benthic systems. Benthic processes dominate the metabolism at the system level, accounting for approximately 70% of total PP and R. Seagrass accounts for about 80% of benthic metabolism. Using an extensive data base for shallow systems, we found that benthic R calculated from O<sub>2</sub> flux represents about 40% of PP. DIC-based estimates of R for Tomales and for San Quintin are almost twice the O<sub>2</sub>-based estimates, providing evidence that sediment respiration is likely to dominate total system respiration in shallow marine systems.

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