

Effect of tidal dynamics on a planktonic community in a coastal lagoon of Baja California, Mexico

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ABSTRACT: Fifty-two water samples were collected from the surface at the entrance of a coastal lagoon for evaluation of microheterotrophic processes. The study was carried out during a period of neap and spring tides over 14 consecutive days. Bacteria, microphytoplankton and zooplankton direct counts were made, along with fractionated respiratory activity. Nutrient, C/N ratio, total organic carbon, particulate organic nitrogen, carbon, seston, dissolved oxygen, particulate silica and chlorophyll *a* determinations were also made. Phytoplankton biomass was low ($9.5 \mu\text{g C l}^{-1}$) and was exceeded by bacterial biomass ($89.4 \mu\text{g C l}^{-1}$) at both spring and neap tides. Bacterial abundance was independent of tidal height and increased with intense water movement at spring tides. Autotrophic production was limited by light penetration and nutrient availability. Most of the respiratory activity in the water column (> 50%) occurred in the $\leq 0.8 \mu\text{m}$ size fraction. Bacterial standing stocks sustained carbon production in the water column. Significant negative correlation between bacteria and nanoplankton suggests a trophic structure dependent on dissolved organic carbon inputs from marsh flora, followed by a trophic chain composed of bacteria, nanoplankton, microzooplankton and *Acartia* sp. It is suggested that food chains stemming from dissolved organic carbon instead of phytoplankton may play a major role in the system since tidal dynamics enhanced bacterial standing stocks during spring and neap tides.

INTRODUCTION

Microheterotrophic organisms, particularly bacteria, play a role not only in mineralization processes but also in organic-matter cycling in marine food chains (Pomeroy 1974, Williams 1981, Azam et al. 1983, Small et al. 1989). Much of this evidence reveals that ca 50% of the organic matter production in the open ocean can pass through bacteria directly. In the pelagic ocean, phytoplankton production is the major source of organic carbon. However this is not always the case in coastal environments where macrophytes and other carbon sources are present, and energy flow occurs predominantly through the decomposer pathway (Newell 1984).

There is some evidence showing the existence of less conventional food webs starting with dissolved organic carbon, followed by bacterial assimilation, protozoan ingestion and the metazoan food web (Gast 1985, Albright et al. 1987, Roman et al. 1988). These processes

may be energetically as important as those based strictly on primary production (Wright 1984, Riemann & Søndergaard 1986, Mann 1988). Ecologically the dissolved organic carbon (DOC) could be more important than particulate organic carbon (POC), so it becomes necessary to understand in detail the relationship between DOC and planktonic communities in coastal ecosystems (Mann 1988).

For one estuary, Painchaud & Therriault (1989) have shown that bacterial biomass may exceed that of phytoplankton and that phytoplankton itself was only a minor carbon source. They also observed that physical factors, such as wind and tidal mixing, can reduce phytoplankton production, thus making bacteria a relatively more important component in the structure and function of the system.

Energy fluxes in coastal ecosystems are highly variable depending on whether the dominant pathways are autotrophic or heterotrophic (Wainright 1987). Resuspended nutrients may take a heterotrophic route

through the planktonic food web, and resuspension in turn will depend on the dynamics of the area and sedimentary characteristics (Wainright 1987).

Resuspension of sediments represents important inputs of both POC and DOC to the water column but its role has been studied in the past mainly as a source of POC for consumers in coastal environments (Woodwell et al. 1977, Turner 1978, Valiela et al. 1978, Imberger et al. 1983, Nixon & Pilson 1983, Knox 1988). Those studies were concerned with the fate of POC but it now appears that the DOC released in the early stages of decomposition may be ecologically more significant (Mann 1988). There is also some evidence showing that in coastal waters there is a link between phytoplankton and heterotrophic bacteria suggesting that phytoplankton production may also be a major substrate for bacterioplankton (Ferguson & Palumbo 1979, Fuhrman et al. 1980, Ducklow 1982).

The role of DOC and POC in the pelagic coastal ecosystems is not clearly understood; for a better understanding it is necessary to consider the processes which influence its variability.

Biological variability in coastal ecosystems is governed mainly by tidal height and tidal amplitude which in turn affect light penetration, nutrient concentration, temperature, salinity and pH (Nixon & Pilson 1983). Biological variability occurs at different time scales (diel, tidal, seasonal cycles), and it is further complicated by spatial variability (Ducklow 1984).

In some coastal lagoons, like those from the west coast of Northern Baja California, plankton production may depend on upwelling events in the nearby area. Consequently high productivity occurs only sporadically (Millán-Núñez et al. 1981, Abrajan-Villaseñor & Alvarez-Borrego 1987). In this area, events of high primary productivity in the water column may take place mainly during summer (Muñoz-Anderson 1989). In contrast, the effect of tidal dynamics in the area will be present more frequently as well as the organic carbon inputs of non-planktonic sources. Thus, it is of interest to investigate if bacterial production may effectively support the trophic structure in these ecosystems during non-upwelling periods. It is also relevant to consider the physical and chemical mechanisms that may control the fluxes of energy in the food web during these events.

To understand how tidal dynamics control the planktonic community we evaluated the variability of total organic carbon (TOC), POC, C/N ratios, seston, nutrients, oxygen, particulate silicon, chlorophyll *a*, respiratory activity, as well as bacteria, microphytoplankton and microzooplankton abundances for a non-upwelling period of 14 d at one station on the coastal lagoon Estero Punta Banda on the west coast of Northern Baja California, México.

MATERIALS AND METHODS

The sampling site was located ca 1.5 km from the entrance to the lagoon (Fig. 1). Samples were taken from surface water exclusively at times of maximum low and high tides. Sampling time fluctuated between 3.5 and 12 h (Fig. 2). Within the 14 sampling days (September 11 to 24, 1987) one period of neap and spring tides was covered. Water temperature and turbidity were recorded at sampling times.

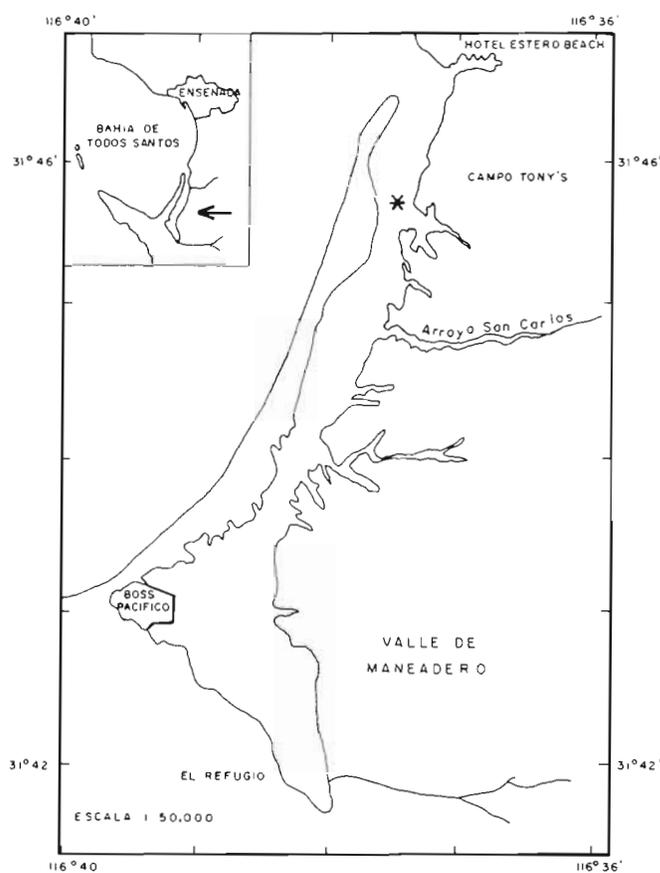


Fig. 1 Study area showing sampling point (star)

Filtering of water for nutrients, seston, chlorophyll *a*, POC and PON was carried out on land immediately after sample collections and the filters were preserved frozen until analysis.

Analysis for nutrients and chlorophyll *a* were done spectrophotometrically following Strickland & Parsons (1972). Particulate biogenic silica (PBS) was determined in 100 ml samples according to Paasche (1980). Samples were hydrolyzed with a dilute solution of sodium hydroxide at 75°C for 2 h, and 5 ml of the hydrolyzate was taken for silicic acid determination according to Strickland & Parsons (1972).

Samples for seston, POC and particulate organic nitrogen (PON) were filtered through previously ashed

Whatman GF/F filters. Analyses of PON and POC were performed in a CHN analyzer (HP-185B) according to Sharp (1974)

Total organic carbon (TOC) analysis was done with a Beckman 915-B carbon analyzer. Carbonates were removed by acidification with HCl and bubbling of the sample with nitrogen gas. Five replicates of 200 μ l sample volume were injected and mean values of replicates were determined.

Microphytoplankton and microzooplankton (20 to 200 μ m) samples were preserved with 3 ml of neutral lugol solution in 300 ml of sample. Occurrence and abundance were determined using the Utermöhl method (Sournia 1978). Microphytoplankton were counted using 25 \times (objective) and 12.5 \times (eyepiece) covering the whole surface of the 50 ml settling chambers. Total nanoplankton (2 to 20 μ m) was estimated using diametric transects according to Utermöhl employing 40 \times (objective) and 12.5 \times (eyepiece). This was used as a minimum estimate of this size fraction since this technique underestimates nanoplankton counts (Davis & Sieburth 1982).

Bacterial abundance was examined using direct counts with epifluorescence microscopy and acridine orange stains (Hobbie et al. 1977). Exactly 10 ml samples were preserved with 0.5 ml concentrated formaldehyde and were counted within 2 wk. Biomass calculations from phytoplankton and bacterial abundances were obtained using conversion factors, 30 μ g C (μ g chl *a*)⁻¹, and 19.8 μ g C (bacterial cell)⁻¹ (Parsons et al. 1984, Lee & Fuhrman 1987, respectively).

Mesozooplankton samples were taken with a 300 μ m

mesh net using vertical hauls exclusively. Counts and identification were done according to Jiménez-Pérez et al. (1988).

Plankton size fractions were prepared by passing water samples first through a 180 μ m plankton net and then through nuclepore filters of 0.8, 3 and 5 μ m pore sizes. A reverse filtration procedure based on Holm Hansen et al. (1970) was used (Morales-Zamorano 1989). The concentrate was discarded and the water used. Plankton size fractions were in situ incubated in dark BOD bottles over a period of ca 6 h. A high precision Winkler method (Bryan et al. 1976, Cajal-Medrano et al. 1987) was used for oxygen analyses.

Variance analysis with one way layout was used to test the significance of variables at low and high tide, and spring and neap tides. In order to confirm increase or decrease in the variables during our sampling period, statistical inference on the slope of the regression line was used. Correlation analysis was done using Spearman's correlation coefficients, and results are given with standard errors at the 95 % confidence level. Polynomial regression analyses were used to compare the tendencies of the variables during high and low tides for the whole sampling period.

RESULTS

Multiple Spearman's coefficient correlation analysis reveals tidal behaviour for seston, oxygen, phosphate and nitrite (Table 1). Seston was correlated significantly with nutrients showing higher values at spring tides with a mean of 46.02 ± 1.3 mg l⁻¹ (Fig. 3a)

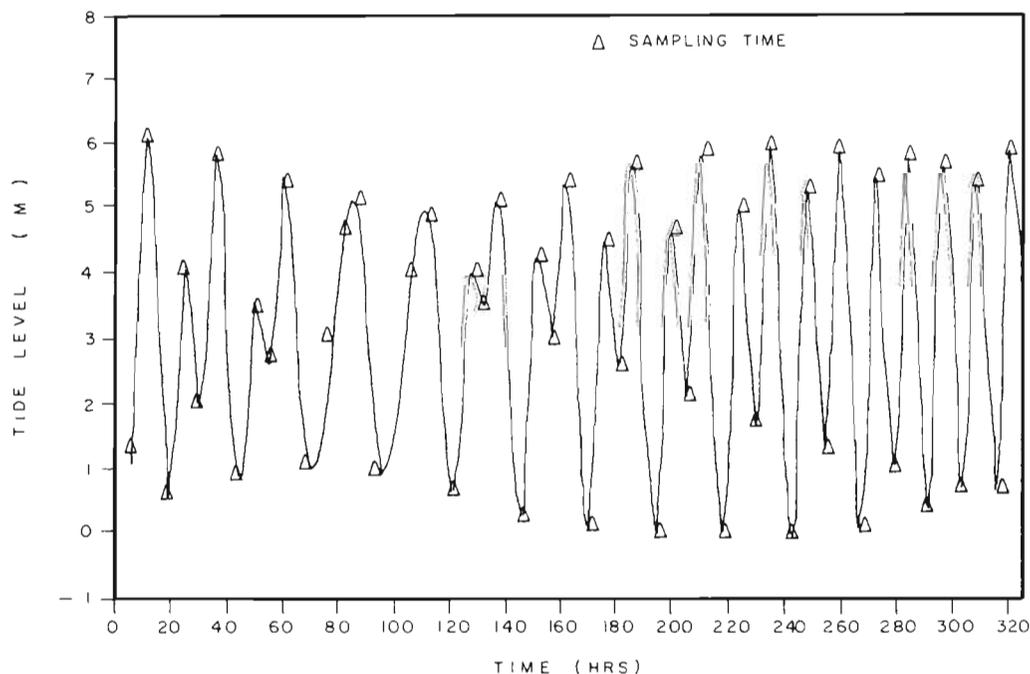


Fig. 2. Tidal height series and sampling time

Significantly higher values were also obtained during spring tides for particulate biogenic silicon ($\bar{x} = 4.3 \pm 0.76 \mu\text{M}$), nitrate ($\bar{x} = 0.18 \mu\text{M}$), and silicates ($\bar{x} = 3.73 \pm 0.358 \mu\text{M}$) (Fig. 3b to d). During high and low tides we found significant differences in phosphates, nitrites,

seston, and oxygen. Higher values were recorded at low tides for phosphates, nitrites and seston (Figs. 3a & 4a, b). Higher oxygen values were generally found at high tides (Fig. 4c), and minimum values at low tides suggesting consumption of oxygen by biological and

Table 1 Spearman's correlation coefficient. Underlined numbers: significance at 95 %

	NO ₃	NO ₂	PO ₄	O ₂	SiO ₂	PSi	POC	PON	C/N	Chl a	Seston	Temp.	Tide
Bact.	.2448	.2615	.0634	-.1407	<u>.5744</u>	<u>.3619</u>	<u>-.3797</u>	-.1976	-.1017	-.1254	.2259	1827	-.1957
NO ₃	→	-.1138	.0922	.0988	<u>.3340</u>	<u>.2678</u>	.0621	1419	-.1510	.2014	<u>.3108</u>	1105	-.0116
NO ₂	→	→	<u>.6302</u>	<u>-.4255</u>	<u>.3991</u>	<u>.0323</u>	-.2047	-.0922	-.2858	-.2515	<u>.3464</u>	.0457	<u>-.5865</u>
PO ₄	→	→	→	<u>-.4019</u>	.2951	-.0458	.0429	1008	-.2071	-.1095	<u>.2981</u>	.0448	<u>-.6218</u>
O ₂	→	→	→	→	-.1518	1048	-.1760	-.1469	1849	-.0807	<u>-.1560</u>	-.1920	<u>.6375</u>
SiO ₂	→	→	→	→	→	<u>.5609</u>	-.2301	-.0121	-.1639	-.2058	<u>.4664</u>	.2961	<u>-.3224</u>
PSi	→	→	→	→	→	→	-.1391	.0640	.0281	-.1352	<u>.4333</u>	1451	-.0692
POC	→	→	→	→	→	→	→	<u>.8993</u>	.2210	-.0721	-.1474	-.0435	-.0920
PON	→	→	→	→	→	→	→	→	-.0614	.0184	-.0160	-.1497	-.1600
C/N	→	→	→	→	→	→	→	→	→	-.0755	-.2280	.3190	.3019
Chl a	→	→	→	→	→	→	→	→	→	→	-.2267	.0902	.0919
Seston	→	→	→	→	→	→	→	→	→	→	→	<u>.1579</u>	<u>-.4311</u>
Temp.	→	→	→	→	→	→	→	→	→	→	→	→	-.0575

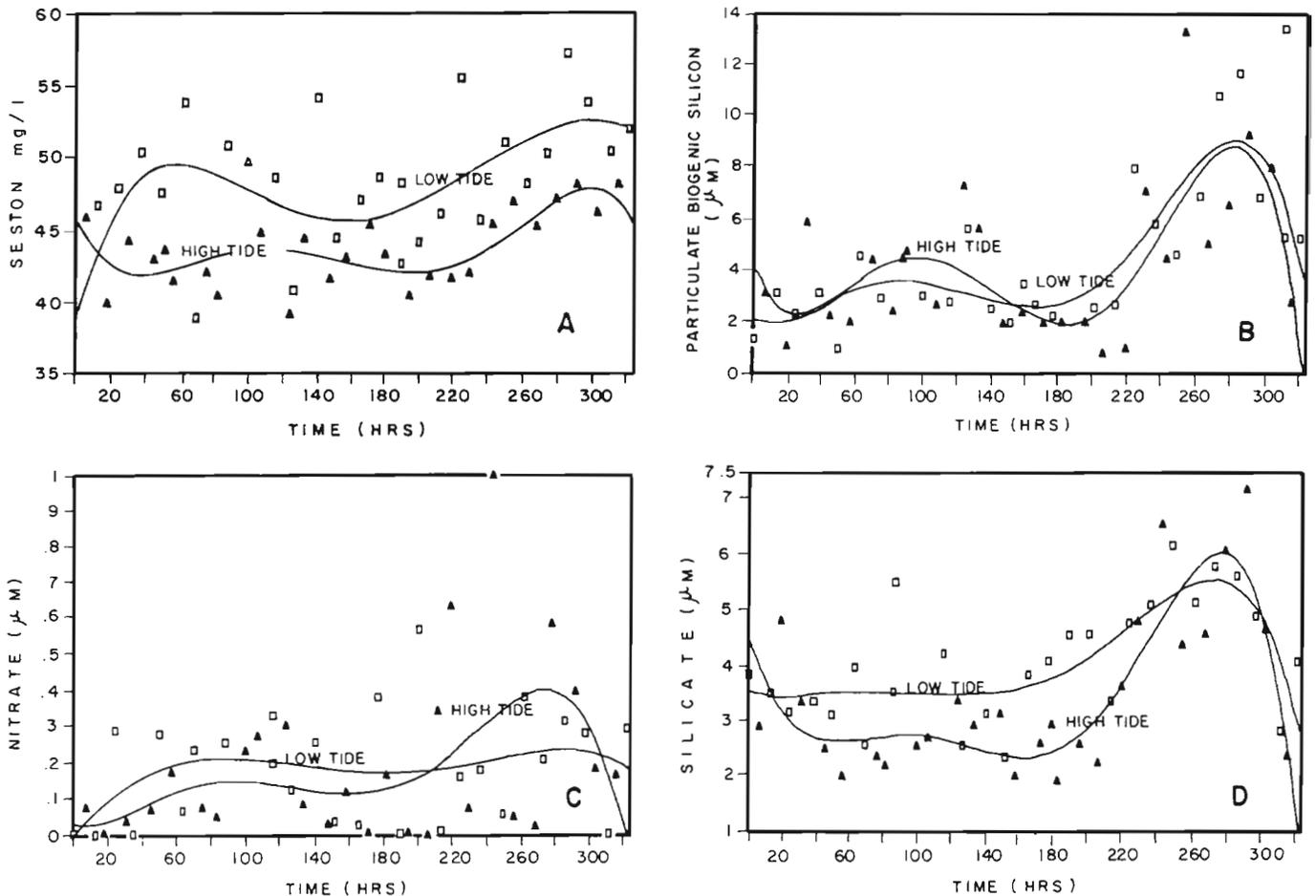


Fig. 3. Tidal variation of seston (a), particulate biogenic silicon (b), nitrate (c), and silicate (d) at low tide and high tide

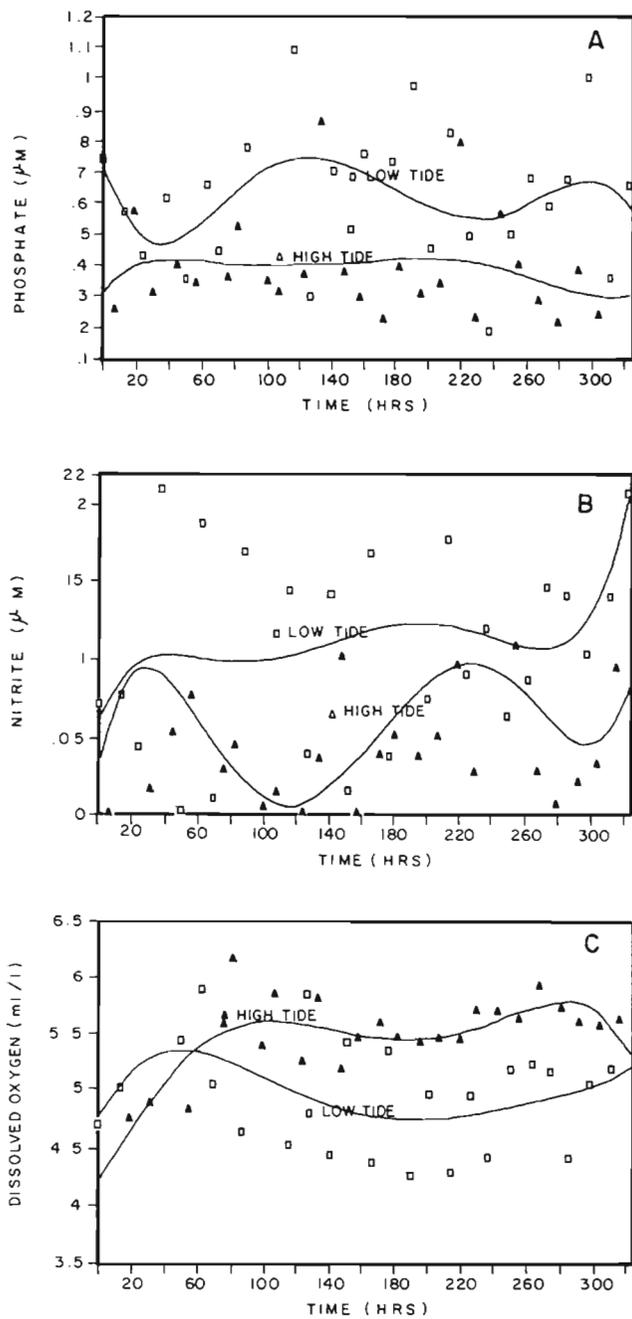


Fig. 4. Tidal variation of phosphate (a), nitrite (b), and dissolved oxygen (c) at low tide and high tide

chemical processes and changes in solubility due to temperature fluctuations.

The variability of the organic material shows a constant C/N ratio for the entire sampling period with mean values of 8.5 ± 0.24 and no significant differences at low or high tides (Fig. 5a). Particulate organic carbon and nitrogen showed lower concentrations during spring tides with mean values of 0.55 ± 0.042 mg C l^{-1} and 0.08 ± 0.007 mg N l^{-1} (Fig. 5b, c). Dissolved

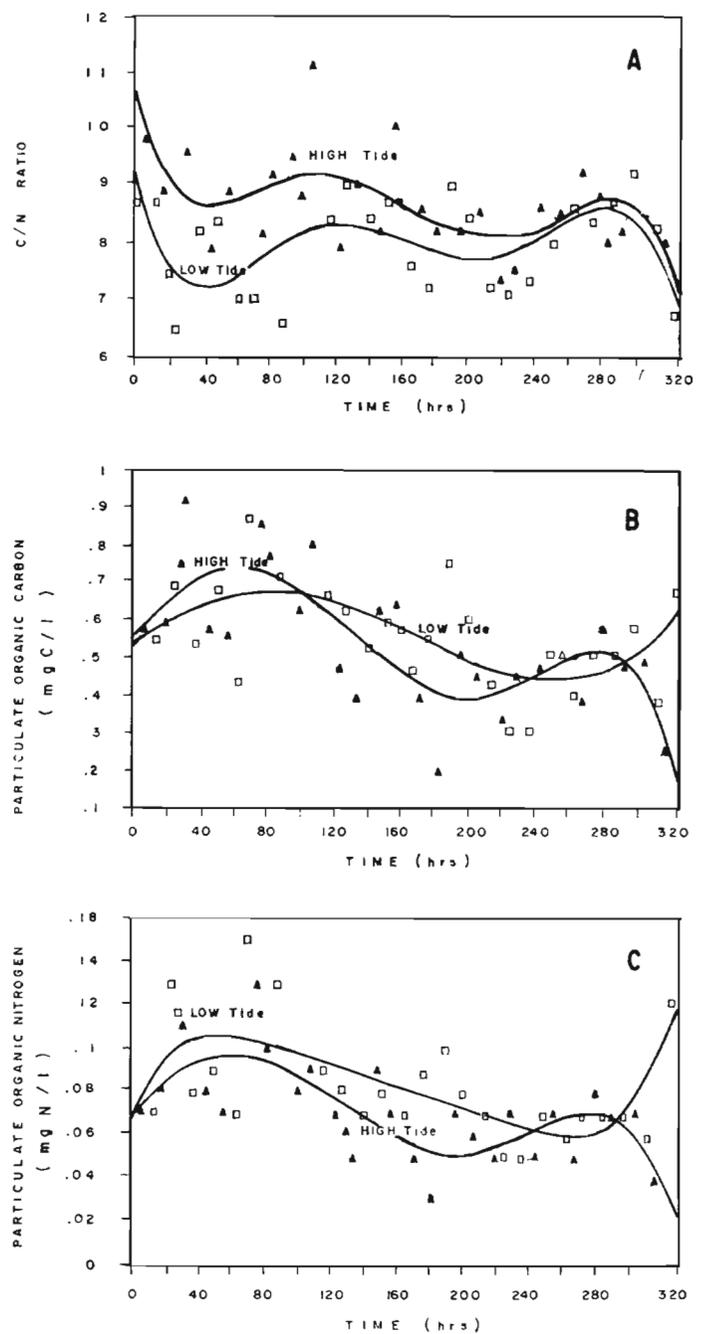


Fig. 5. Tidal variation of C/N ratio (a), particulate organic carbon (b), and particulate organic nitrogen (c) at low tide and high tide

organic carbon concentrations were calculated from TOC and POC samples and revealed a mean value of 3.2 ± 0.49 mg C l^{-1} ($n = 19$) and a mean DOC/POC ratio of 6 for the whole sampling period.

Cumulative respiration documents that the size fraction $< 0.8 \mu m$ respired $56.4 \pm 18.8\%$ ($n = 5$); size fraction $< 3.0 \mu m$, $76.6 \pm 7.7\%$ ($n = 8$); size fraction $< 5 \mu m$, $96.9 \pm 3.7\%$ ($n = 13$); the remaining 3.1% by

the fractions greater than 5 μm but smaller than 180 μm (Fig. 6).

Chlorophyll a was not affected by tides; mean values of only $0.3 \pm 0.05 \text{ mg m}^{-3}$ were found. At present, these

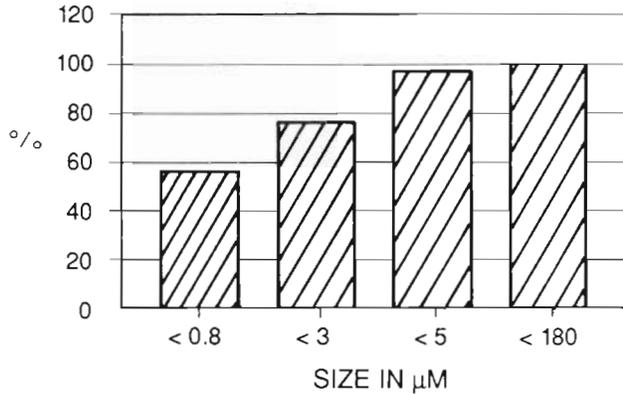


Fig. 6. Cumulative respiration in plankton size fractions

values are the lowest reported for the study area (Fig. 7a). High values of pheophytin were also detected only during spring tides ($2.9 \pm 0.88 \text{ mg m}^{-3}$). Microphytoplankton (2 to 200 μm) abundance was very low (2.2 to 7 cells ml^{-1}) but it is within the low end of other reported values (Alvarez-Borrego & Najera-Muñoz 1979). During high tides the highest microphytoplankton abundance was observed ($\bar{x} = 5.6 \pm 1.4 \text{ cells ml}^{-1}$), dinoflagellates being the most abundant group. Bacterial abundance was significantly higher at spring tides (overall mean = $4.5 \pm 0.39 \times 10^6 \text{ cells ml}^{-1}$) and was not affected by low and high tides (Fig. 7b). The bacterial to microphytoplankton cell ratio ranges from 1.4×10^5 to 4.5×10^5 (Table 2). These ratios are 2 orders of magnitude higher than in other coastal areas (Azam & Ammerman 1984).

Bacterial abundance and chlorophyll content were converted to carbon using factors of Lee & Fuhrman (1987) and Parsons et al. (1984). From these estimations it can be seen that bacterial contribution to POC was

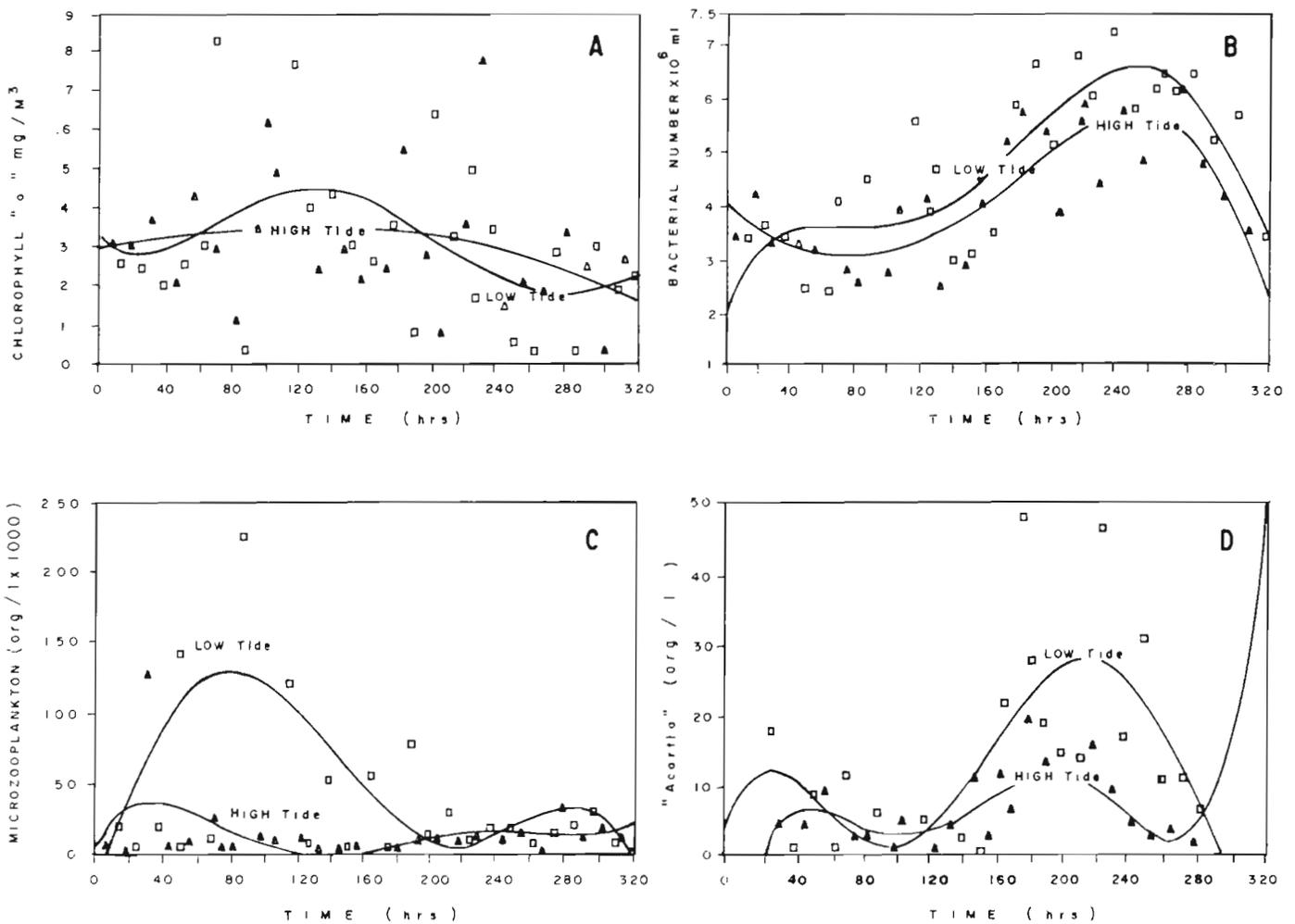


Fig. 7. Tidal variation of chlorophyll a (a), bacterial abundance (b), microzooplankton (c), and *Acartia* sp. (d) at low tide and high tide

Table 2. Relative abundances at Estero de Punta Banda during spring and neap tides

Group	Neap tides		Spring tides		Mean ratios	
	Range (Organisms ml ⁻¹)	Mean	Range (Organisms ml ⁻¹)	Mean	Bact./ Phyto.	Microzoopl./ Phyto.
Bacteria	(1.2–5.6)10 ⁶	3.4 × 10 ⁶	(3.6–7.3)10 ⁶	5.6 × 10 ⁶	Our study: 6 × 10 ⁵	1.8
Nanoplankton	2–366	108	3–148	47		
Tintinnids	0.06–37	4	0.04–8	1	Azam & Ammerman (1984): 1 × 10 ³	1 × 10 ⁻¹
<i>Acartia</i> sp.	(4.6–233)10 ⁻⁴	65 × 10 ⁻⁴	(3–488)10 ⁻⁴	15 × 10 ⁻⁴		

Table 3. Relative contribution of phytoplankton and bacterial biomass to particulate organic carbon

Organic pools	Concentration (µg C l ⁻¹)	Percentage
Phytoplankton	9.5	2
Bacteria	89.4	16
Total POC	550.0	100

roughly 9 times greater than the microphytoplankton contribution (Table 3).

The use of settling chambers in nanoplankton (2 to 20 µm) counts underestimates the abundance of this size fraction (4 to 30% of the cells as detected by epifluorescence microscopy; Davies & Sieburth 1982). In spite of that, significant negative correlation was observed between total nanoplankton abundance and bacterial abundance.

The highest microzooplankton densities were present during low tides ($\bar{x} = 3.0 \pm 1.7$ cell ml⁻¹; Fig. 7c). Mesozooplankton (0.3 to 2 mm) mean densities were higher at low tides (16 individuals l⁻¹) than at high tides (9 individuals l⁻¹), and mean values of 13 organisms l⁻¹ for both periods. *Acartia* sp. was conspicuously present throughout the sampling period, representing 90% of net zooplankton during the whole study (Fig. 7d, Table 2).

DISCUSSION

The general pattern of seston, particulate silicon and nitrate indicates greater resuspension of sediments during spring tides. However, short time-scale events like high and low tides also show significant differences in mean values of seston, phosphate and nitrite, suggesting sediment resuspension during these events (Valiela et al. 1978, Knox 1988). Particulate biogenic silicon concentration was relatively high when compared to the Southern California Bight (Orellana-Cepeda et al. 1990), probably because our study area is

shallower. Nutrient concentrations during spring tides were highest for nitrate and silicate. Also higher values were found for nitrite and phosphate during low tides. This suggests that mineralization takes place mainly in sediments and that ammonium, nitrite and phosphates are released as the first by-products to the overlying water. This process influences the water column mainly at low tides. High concentrations of ammonium should be expected since very high (19 to 1970 µM) concentrations in pore waters have been reported for this lagoon (Camacho-Ibar & Alvarez-Borrego 1988). Nitrate is the end product of mineralization and is present in higher concentrations when highest resuspension of sediments takes place at spring tides. Silicates show significant increases in concentration at spring and low tides, indicating also that their concentrations depend on resuspension of sediments. This is also evident from the significant correlation with particulate silicon.

Dissolved oxygen variability is not related to long-term scale events like spring and neap tides. On the contrary, this variable was controlled by physicochemical and biological processes during shorter events like high and low tides.

The concentration of POC was low and similar to that found by Eppley et al. (1977) in the Southern California Bight during low nitrate conditions (< 1 µM). The POC content decreased during spring tides because of the presence of a larger water volume off the lagoon when the mean water level increased. Because POC was negatively correlated with bacteria it is suggested that higher concentrations of POC stem from a different source. The most likely sources of POC and DOC in the area are marsh vegetation like *Spartina* spp. and edaphic algae (Sullivan & Moncreiff 1990) which could provide the basis for a detritus food chain. In this case the trophic web must be strongly associated with heterotrophic microorganisms. When the contribution of our biomass estimates are compared, in terms of carbon, it can be seen that phytoplankton biomass is much lower (2%) than bacterial biomass (16%). Moderate

variability of the low C/N ratios and a slight decrease in it during spring tides suggest that bacteria might enrich the nitrogen content of the particles, since their abundance increases at spring tides. Other studies near our study area have revealed wide variations of C/N ratios in salt marshes (Lara-Lara et al. 1980). These authors reported C/N ratios of 3 to 81 associating the lowest ratios to phytoplankton and bacteria. Hence it is possible that bacterial abundance in the present study masked the high C/N ratios of *Spartina* spp. (20 to 63; Harrison & Mann 1975) and therefore provided high-quality biomass for consumers (Wainright 1987).

Bacterial abundance in the water column increased during spring tides due to resuspension of sediments and inputs of labile substrate. Although we did not estimate the amount of labile carbon, DOC mean value was high (3.2 mg C l^{-1}) suggesting continuous inputs of substrate. Pheophytin values were high during spring tides and cannot be explained from our low chlorophyll *a* data, hence we presume that macrophyte leacheates are the source of DOC as reported by Imberger et al. (1983) for a southeastern US salt marsh estuary. Bacterial standing stocks increased at spring tides, when the greater water volume off the lagoon reduced the POC content. At this time C/N ratios slightly decreased, presumably due to the presence of bacterial cells. Bacterial standing stocks were not correlated with seston but revealed tidal-dependent behaviour. So, it is also possible that resuspended sediments promoted bacterioplankton growth (Wainright 1987).

Microphytoplankton abundance was the lowest reported for the study site, however low direct counts are coherent with low chlorophyll *a* values. It has been suggested that bacteria and algae are the most abundant organisms in coastal surface seawater with a ratio of 10^3 bacterial cells to 1 phytoplankton cell (Azam & Ammerman 1984). The ratio found in our study ($10^5:1$ bacteria to microphytoplankton) shows how variable the coastal lagoon environment can be. Although we do not know how often such a situation may occur, evidence for a similar situation was found by Painchaud & Therriault (1989) in an estuarine environment.

Production in coastal lagoons derives from photosynthetic producers, macro and microalgae (Knox 1986) or vascular plants (Moran & Hodson 1989). Microalgae production in this coastal lagoon may be restricted by light penetration. Two days before our study started, primary productivity was measured by the ^{14}C technique showing the lowest reported value for this lagoon ($0.8 \text{ mg C m}^{-3} \text{ h}^{-1}$; Muñoz-Anderson 1989). Therefore biomass production in the water column would seem to be primarily supported by bacterial production based on DOM from detrital macrophytes. Metabolic activity experiments show that our microheterotrophic community was active, respiring a major

portion of the organic carbon into the water column, and that bacteria were quantitatively the main consumers of oxygen. At first approximation our respiration results document that bacteria respired $11.1 \text{ mg C m}^{-3} \text{ h}^{-1}$ on average. Even though carbon conversion efficiency for bacteria is variable (Newell et al. 1981, Newell 1984, Williams 1984), when a range of 30 to 80 % is assumed we obtain 3.3 to $44 \text{ mg C m}^{-3} \text{ h}^{-1}$ as an approximation of bacterial production. A mean net community production of $12.2 \text{ mg C m}^{-3} \text{ h}^{-1}$ was obtained during our study via the oxygen technique (data not shown). This rough estimation indicates that bacterial production may exceed that of microphytoplankton when their abundance is low, or may be comparable to it during periods of high primary productivity in summer. Primary production by phytoplankton insufficient for microheterotrophs has also been found in other ecosystems (Smith et al. 1986, Painchaud & Therriault 1989) suggesting inputs of organic matter from other sources. However, the accuracy of our estimations is limited, by assumptions regarding bacterial carbon conversion efficiency.

In any event, our respiration data show that the bacterial community in our study was the major metabolic component.

Significant negative correlation between bacteria and nanoplankton, and the dominance of *Acartia* sp., strongly suggest a heterotrophic food web stemming from organic carbon produced by macrovegetation and transferred by bacteria to other trophic levels (Heinbokel & Beers 1979, Takx & Polk 1982, Sieburth 1984, Sherr et al. 1986, Roman et al. 1988). It is likely that microzooplankton constitute the principal diet of *Acartia* sp. along with detritus associated microorganisms as our high numbers of tintinnids suggest (Robertson 1983, Gifford & Dagg, 1988).

Pheophytin data suggest that organic carbon from marsh areas caused the increase in bacterial abundance which occurred mainly at spring tides. In contrast, no statistical difference was found in bacterial abundance during low and high tide. Dilution of bacterial abundance with larger volumes of oceanic water at high tides was not observed. This is probably due to rapid bacterial response to organic substrate supply during spring tides.

The data presented here underline the importance of microheterotrophic processes based on DOC from marsh areas as a feasible support of planktonic food web in our study area (Fig. 8) promoted via sediment resuspension by tidal forces. It is of interest to determine the extent of the temporal persistence of this phenomenon.

Primary productivity studies in the area (Millán-Núñez et al. 1981, Abrajam-Villaseñor & Alvarez-Borrego 1987) show that fertilization processes by upwelling may be an important mechanism for production in

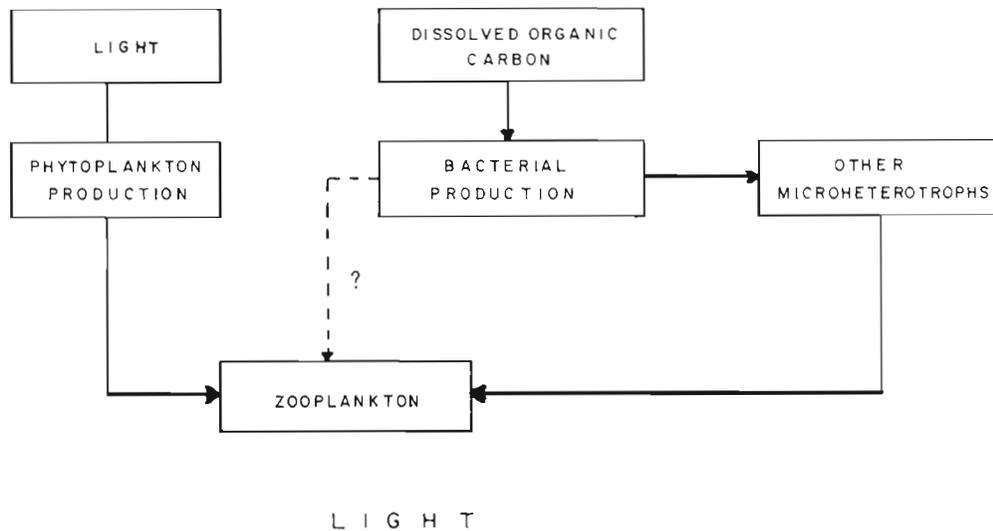


Fig. 8. Conceptual model of trophic interactions at Estero de Punta Banda (after Cajal-Medrano 1990)

the water column. Nonetheless, its occurrence is limited in space and time so the mechanisms of production suggested here may be operating more often than previously thought, and are forced by higher frequency variables like tidal energy.

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