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Impact of two decades of shellfish farming on phytoplankton biomass, abundance and productivity of a coastal lagoon influenced by upwelling

Impacto de dos décadas de ostricultura en la biomasa, abundancia y productividad fitoplanctónica de una laguna costera influenciada por surgencias

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ABSTRACT

Long-term impact of the Pacific oyster *Crassostrea gigas* farms on the phytoplankton biomass as chlorophyll *a* concentration (chl-*a*), abundance and productivity (PP) of the western arm of Bahía San Quintín (Falsa Bay), a coastal lagoon influenced by the California Current coastal upwelling, was evaluated after two decades of commercial cultures. High-resolution time series (on an hourly basis) of these variables were generated in 1999 and 2000, for locations with and without oyster cultures in Falsa Bay. Representative averages of these data were compared with data reported for 1979, when the commercial cultures were just starting. Also, data of 1979 and recent data were used separately to explore possible short-term (hourly) effects of oysters on the phytoplankton variables. The available data are scarce and do not support the hypothesis of diminished phytoplankton biomass, abundance and PP due to the oyster cultures. In general, there were no statistically significant differences between the averages of chl-*a* (2.5 mg m^{-3}), microphytoplankton abundance (from $42 \cdot 10^3$ to $194 \cdot 10^3$ cells L^{-1}, depending upon the location) and PP (12 mgC m^{-3} h^{-1}) when comparing 1979, and 1999 - 2000 data. This was possibly due to the relatively low residence time of Falsa Bay waters (~8 days) and relatively low oyster density (a total of ~900 tons, with an estimated maximum carrying capacity from ~2,000 to 6,000 tons for this arm of the bay).

Key words: Shellfish farming; *Crassostrea gigas*; phytoplankton; California Current; coastal lagoon.

RESUMEN

Se evaluó el impacto de las granjas de ostión del Pacífico *Crassostrea gigas* tanto en la biomasa como en la concentración de clorofila *a* (chl-*a*), abundancia y productividad fitoplanctónica (PP) del brazo occidental de Bahía San Quintín (Bahía Falsa), una laguna influenciada por las surgencias costeras de la Corriente de California, después de dos décadas de cultivos comerciales. En 1999 y 2000 se generaron series de tiempo de alta resolución (horas) de estas variables en Bahía Falsa. Se compararon promedios representativos de estos datos con los de datos reportados para 1979. Ambos conjuntos de datos también se utilizaron separadamente para explorar efectos de corto período (horas) de los ostiones. Los datos disponibles son muy escasos y no apoyan la hipótesis de una disminución de la biomasa, abundancia y PP fitoplanctónicas debido a los cultivos de ostión. En general no hubo diferencias estadísticas significativas entre las medias de la concentración de chl-*a* (2.5 mg m^{-3}), abundancia de microfitoplancton (de 42 $\cdot 10^3$ a 194 $\cdot 10^3$ células L^{-1}, de acuerdo a la localidad) y PP (12 mgC m^{-3} h^{-1}) al comparar las de 1979 con las de 1999 - 2000. Esto posiblemente se debió al relativamente bajo tiempo de residencia de las aguas de Bahía Falsa (~8 días) y a la relativa baja densidad de ostiones en cultivo (~900 toneladas en total, con un máximo estimado de carga de ~2,000 a 6,000 toneladas para este brazo de la bahía).

Palabras clave: Cultivo de ostión; *Crassostrea gigas*; fitoplancton; Corriente de California; laguna costera.

INTRODUCTION

Impact of shellfish farming on the environment has been one of the most debated issues concerning the sustainability of aquaculture in the last decade. Modifications of benthos (Crawford *et al*., 2003), vertical flux of materials (Proenca & Schettini, 1998), light transparency (Newell *et al*., 1999), and biochemical cycles (Souchu *et al*., 2001) have been detected. The latest studies have been conducted in order to evaluate the effects of shellfish activities on phytoplankton productivity (PP) (Souchu *et al*., 2001), size fractions (Dupuy *et al*., 2000) and composition (Cognie *et al*., 2001), since phytoplankton represents the main food item of filter-feeder bivalves (Jones & Iwama, 1991). Most of this research has been actually derived from controlled experiments using the Pacific oyster, *Crassostrea gigas* (Thunberg 1793) (Knuckey *et al*., 2002). Based on 30-minute incubations, Dupuy *et al*. (2000) suggested that structure of phytoplankton community changes to smaller fractions in waters influenced by significant stocks of *C. gigas* since picophytoplankton cells (<1 μm) cannot be retained by oyster gills.

Also, bulk *in situ* measurements revealed that cultivated areas of *C. gigas* can be associated with deficit of phytoplankton biomass, estimated as chlorophyll *a* concentration (chl-*a*), and phytoplankton productivity (PP) in water bodies with relatively large flushing times (months) and high densities of bivalves (Souchu *et al*., 2001). On the other hand, field observations in very dynamic environments (tidal currents up to ~1 m s^{-1}) have shown no significant seasonal effects of oysters on chl-*a* and PP (Kaspar *et al*., 1985). Nevertheless, changes of phytoplankton biomass (chl-*a*), abundance and PP throughout long periods of time (decades) have not been analyzed for places with oyster cultures. And, at the other end of the spectrum, there have been no *in situ* studies of this kind of changes for short temporal scales such as during a tidal cycle. Bahía San Quintín is a coastal lagoon ~300 km south of the USA-Mexico border (San Diego). It is strongly influenced by the California Current System coastal upwelling. The main fertilization mechanism of the lagoon is the combination of tidal currents and coastal upwelling, and this can be detected even in the inner arms (Alvarez-Borrego, 2004). The lagoon hosts one of the most productive *C. gigas* set of farms of Mexico (García-Esquivel *et al*., 2004). Due to the interplay of these factors, it is not possible to conclude *a priori* about short or long term effects of shellfish cultures on the phytoplankton of this lagoon.

The objective of the present study was to estimate the long-term impact of *C. gigas* farms on the phytoplankton characteristics of Bahía San Quintín after two decades of commercial oyster culture (1979-2000). Also, both our 1999 and 2000 time series and data from the literature were used to explore the possibility of significant differences of phytoplankton characteristics between ebb and flood flow at each location. The basic hypotheses are: the average phytoplankton biomass (chl-*a*), abundance, and PP have decreased significantly from 1979 to 1999 - 2000; the average of phytoplankton abundance is lower with ebb flow than with flood flow; and the <10 μm phytoplankton fraction contributes more to the total biomass in ebb than in flood flow.

MATERIAL AND METHODS

Physical and chemical characteristics of Bahía San Quintín and the effect of El Niño events are discussed in detail by Alvarez-Borrego (2004) and Silva-Cota and Alvarez-Borrego (1988). Briefly, the lagoon is a 49 km^2 "Y" shaped embayment (Fig. 1). The western arm is called Falsa Bay (FB). Seagrasses cover ~43% of the areal extent of the lagoon (Ward *et al*., 2004). Tides have a strong semidiurnal component and maximum range is ~2.5 m. Vertical distribution of water properties is generally homogeneous due to turbulence caused by tidal currents and winds (Millán-Núñez *et al*., 1982).

In this study, time series were generated at three locations in Falsa Bay (FB) during spring tides in 1999 and 2000. Surface water samples were obtained from boats, using 2 L Niskin bottles. Samplings were performed on 15-16 June 1999, on 7 April 2000, and on 12 June 2000. To evaluate the long-term effect of *C. gigas* cultures on the phytoplankton variables of Bahía San Quintín, Millán-Nuñez *et al*. (1982) data (June 25 through July 5, 1979) were compared to our 1999 and 2000 data. The two locations of Millán-Núñez *et al*. (1982) study that are of interest to us (hereafter FB1' and FB3') were in the channel (Fig. 1). Their sampling and laboratory methods of analysis were very similar to ours. Millán-Nuñez *et al*. (1982) data were also used to explore the possibility of significant differences of phytoplankton characteristics between ebb and flood flow at each location, to complement the results from the 1999 – 2000 data. Daily Bakun Upwelling Index (UI) values were obtained for the oceanic area off Bahía San Quintín and for all sampling periods, including that of Millán-Núñez *et al*. (1982) (http://www.pfel.noaa.gov).

On 15-16 June 1999, sampling was done every hour (chl-*a*, phytoplankton abundance, PP and light attenuation) and every two hours (zooplankton grazers). Surveys were conducted simultaneously at locations FB1, at the outer limit of the oyster culture, and at FB2 in the oyster-cultivated area (Fig. 1). Most samples were taken from 12:00 (15/06/1999) to 08:00 h (16/06/1999). Samples for PP incubations were collected only at location FB2, and from 07:30 through 17:30 h (15/06/1999). Productivity ^{14}C incubations were performed every hour and each one lasted 30 minutes. Total and <10 μm chl-*a* fractions were measured for FB2.

On 7 April 2000, sampling started at 8:30 and finished at 17:30 h, and PP incubations were run from 08:30 to 17:30 at both locations, FB1 and FB2. To estimate PP for the <10 μm fraction, filtration was done after the incubations. Total and <10 μm chl-*a* fractions were measured for FB1 and FB2. On 12 June 2000, sampling lasted from 6:30 to 18:30 h, and a third sampling location was chosen in the inner part and in the main channel where there were no adult oysters (FB3). For this last sampling, PP incubations were only performed for FB1, and besides the <10 μm fraction, chl-*a* and PP data for the 10-20 μm and the >20 μm size fractions were also produced. Total, <10 μm and 10-20 μm chl-*a* fractions were measured for FB1, FB2 and FB3. For each sampling, surface and submarine light (PARz) values were obtained with a light-meter LiCor (LI-190SB, LI-192SB). Linear regressions of $\ln(PAR_{0.5m}\ PAR_z^{-1})$ versus z were run to estimate the average coefficient of vertical light attenuation (K_{PAR}) as the slope (Lambert-Beer's law).

For each chl-*a* sample (100 ml), phytoplankton fractions were obtained with 20 μm and 10 μm Nitex mesh. Samples for total and fractioned chl-*a* were then filtered in the field through

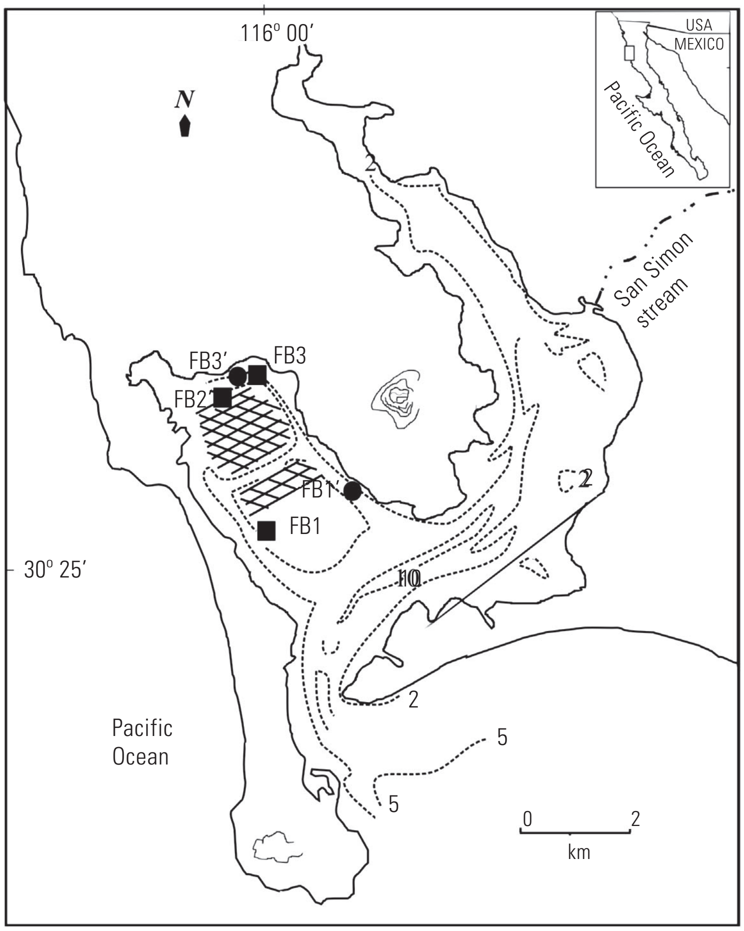

Figure 1. Sampling locations at San Quintin Bay. Broken lines indicate the outer limits of the main channel and the numbers are depth in m. The western arm is Falsa Bay (FB). Locations for the 1999 and 2000 time series are indicated with dark rectangles, and those for the 1979 time series with dark circles. Hatched areas have *C. gigas* cultures.

Whatman GF/F glass fiber filters, using a manual vacuum pump. Filters were frozen and kept in liquid nitrogen until ready for analysis. In the laboratory, filters with chlorophyll samples were extracted during 24 h under dark conditions with 90% acetone. Pigment concentration was measured by fluorometry and estimated according to Venrick and Hayward (1984). Surface water for PP incubations was collected with a bucket. Three light and three dark replicates were inoculated with ^{14}C (1 µCi each) and incubated *in situ* underneath the sea surface (0.3 m) in glass vials (25 ml) during 30 minutes. After incubation, phytoplankton fractions for PP were obtained with 20 µm and 10 µm Nitex mesh. Incubated samples for total PP and the fractions were then filtered through 0.45 µm cellulose ether filters (GN-6, 25 mm diameter, Metricel, Gelman Sciences). Filters were frozen in liquid nitrogen. At the laboratory, filters were acidified during 8 hours with HCl vapor and placed in glass vials with 10 ml of ECOLITE(+) scintillation cocktail. Radioactivity was counted with a liquid scintillation counter (Beckman LS-100C) and the calculation of carbon uptake was done following Strickland and Parsons (1972). Size fractions were calculated by difference as: (>20 µm) = total –(<20 µm); (10-20 µm) = (<20 µm) – (<10 µm).

Samples for quantifying microphytoplankton (diatoms and dinoflagellates) abundance (100 ml) were fixed with Lugol's iodine fixative (5%), and in parallel net samples were taken with a conic net 22 µm mesh size. Every net cast was done holding it from the anchored boat and letting the tidal current do the filtration for 15 minutes. Net samples were fixed with 6% formaline. Phytoplankton and grazers (copepod nauplii and loricate tintinnids) abundance was estimated with an inverted microscope (Utermöhl, 1958). Dominant micro-phytoplankton taxa were defined as those contributing > 50% of total abundance in the sample. Diatom and dinoflagellate identification was done following Hernández-Becerril and Alvarez-Borrego (1983) and Siqueiros-Beltrones and Ibarra-Obando (1985).

Short-term averages of phytoplankton variables (chl-*a*, diatom and dinoflagellate abundance and PP) were compared as a function of location and tidal condition (ebb flow – flood flow) with a two way ANOVA test (with replication). This was done separately using Millán-Núñez *et al*. (1982) data, and our 1999 and 2000 data. Also, additional comparisons of K_{PAR}, chl-*a* and PP fractions, copepod and tintinnids abundance were performed for each date with our 1999 and 2000 data. Statistical significance of long-term phytoplankton modifications between 1979 and 1999-2000, was evaluated comparing daily averages of chl-*a*, microphytoplankton abundance and PP for the outer and inner part of Falsa Bay separately, and considering the same tidal condition (spring tides). Specific differences were examined with a Tukey test for multiple comparisons of means. Before the ANOVA, variables were log-transformed and homogeneity of variances was checked using a F-test (Sokal & Rohlf, 1995).

RESULTS

On all sampling dates of 1999 and 2000, average chl-*a* did not show significant differences between ebb and flood flow ($p > 0.05$; Fig. 2). In June 1999 and in April 2000 there were no significant differences between locations. In June 2000, the average chl-*a* for FB1 was significantly larger than those for FB2 and FB3 during both flood and ebb flow ($p = 0.02$). On this last sampling date, there were no significant differences between the FB2 and FB3 chl-*a* averages for the two tidal conditions ($p > 0.05$). When comparing the chl-*a* averages for 1999 and 2000 with those of 1979 (from Millán-Núñez *et al*., 1982: 2.51 and 2.55 mg m^{-3} for FB1' and FB3' respectively), we found that only those for June 2000 were significantly lower than those for the 1979 data ($p < 0.01$).

The average of microphytoplankton abundance for FB1 was higher than that for FB2 in 1999 and 2000 (Fig. 3). The most pronounced difference between the two locations was obtained for 1999 (t = 3.90, $p < 0.01$, n = 11). No significant differences could be detected between ebb and flood flow, for each sampling site. In June 2000, with exception of one outlier with very high abundance, there was no significant difference between the averages for FB2 and FB3. Comparisons of the average abundance of microphytoplankton between 1979 and 1999 and 2000 showed no statistical significant differences.

No significant differences between the averages of total PP, for June 1999 and April 2000, were detected when comparing flood and ebb flow for the same location (Fig. 4). In April 2000, in accordance with phytoplankton abundance, average PP for FB1 was significantly higher than the one for FB2 (t = 3.84, $p < 0.01$, n = 10) (this was the only date with PP values for both locations, Fig. 4b). In general, when comparing the inner part of Falsa Bay, total PP average value for June-July of 1979 (FB3') was not significantly different from that of June 1999 (FB2) (t = 2.10, $p < 0.01$). Also, when comparing the entrance to Falsa Bay, the average PP value for June-July of 1979 (FB1') was not significantly different from that of April 2000, but it was higher than the one for June 2000 (FB1).

No significant differences were found for K_{PAR} when comparing flood and ebb flow, and when comparing locations (Table 1, $p > 0.05$), with exception of location FB2 in June 1999 and location FB1 in April 2000 where flood flow had significantly higher K_{PAR} average values than those for ebb flow. In June 1999, there were no significant variations of the average values of the <10 µm chl-*a* fraction (both, absolute values and the percentage) with tidal flow ($p > 0.05$; Table 1). The same was found for April 2000 when considering the absolute average values. Nevertheless, there was a higher percent contribution of this chl-*a* fraction during ebb than during flood flow at both the inner and outer locations. In June 2000, the <10 µm chl-*a* fraction was in general greater for the inner location FB3 than for the other two locations, and this fraction did not show an effect of tidal flow in the inner part of Falsa Bay, but it was greater with flood than with ebb flow at FB1 (Table 1; two-

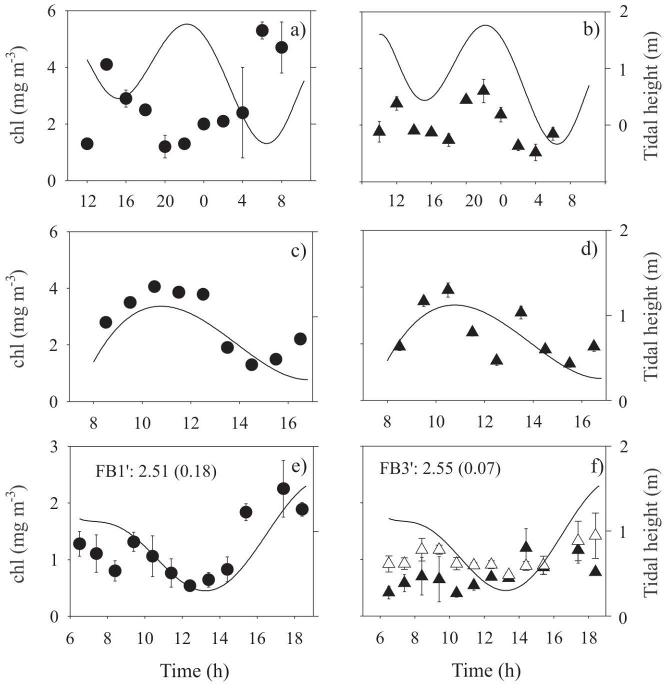

Figure 2. Short-term time series of chlorophyll *a* (chl-*a*). Solid circles represent location FB1, solid triangles FB2, and clear triangles FB3. a-b) June 15-16, 1999; c-d) April 7, 2000; e-f) June 12, 2000. Vertical bars are the standard error, which are not shown when they are smaller than the symbols. The chl-*a* averages (and standard error) for locations FB1' and FB3' of the 1979 (Millán-Nuñez et al., 1982) time series are the numbers in the upper left corners of panels e and f, respectively. Sea level changes are shown with continuous lines, in each case.

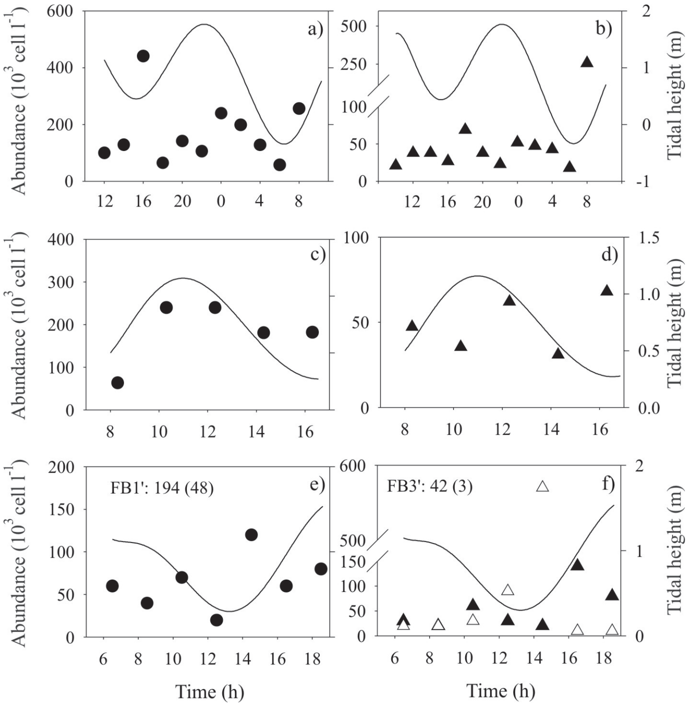

Figure 3. Time series of phytoplankton abundance (diatoms + dinoflagellates). Notice that the vertical scales are different. Solid circles represent location FB1, solid triangles FB2, and clear triangles FB3. a-b) June 15-16, 1999; c-d) April 7, 2000; e-f) June 12, 2000. Standard error bar for each data point is smaller than the symbol. Numbers in the side left of the panel are the average and standard error (between parenthesis) of the microphytoplankton abundance (diatoms + dinoflagellates) for each location of the 1979 time series of Millán-Nuñez *et al.* (1982).

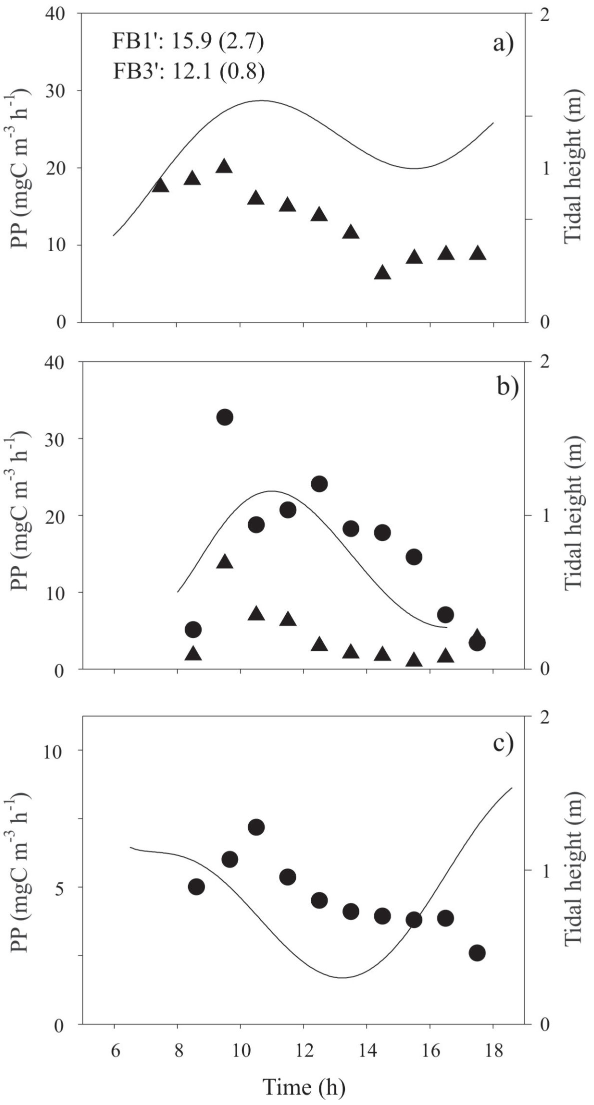

Figure 4. Short-term time series of total phytoplankton productivity. Notice that the vertical scale of panel c for PP is different. Solid circles represent location FB1, solid triangles FB2. a) June 15, 1999; b) April 7, 2000; c) June 12, 2000. Standard error bar for each data point is smaller than the symbol. Numbers in the side left of the panel are the average and standard error (between parenthesis) of PP at each location of the 1979 time series of Millán-Nuñez *et al.* (1982).

way ANOVA, F = 20.1, p <0.01, n = 5). In general, the percentage of the <10 µm chl-*a* fraction was higher over the area with oyster cultures than at FB1. The intermediate chl-*a* fraction (10-20 µm) average values were similar for FB1 and FB3, and it was highest for FB2 and with flood flow (Table 1). On the other hand, the chl-*a* fraction for cells >20 µm had average values that were highest for FB1, and they had similar low values for the two inner locations, FB2 and FB3. Contribution of the >20 µm average chl-*a* fraction to the whole sample was largest at the entrance to Falsa Bay (FB1), and its absolute value decreased with ebb flow.

There was no significant influence of tidal flow on the <10 µm PP fraction absolute averages of June 1999, in the inner part of Falsa Bay (FB2; Table 2). In April 2000, the <10 µm PP fraction absolute averages were higher for FB1 than for FB2 during ebb flow (t = 2.84, p <0.01, n = 10), but there was no significant difference between the two locations during flood flow. In June 2000, the <10 µm PP fraction average was higher for ebb than for flood flux; the 10-20 µm PP fraction average had no clear relation with tidal flow; and the phytoplankton >20 µm had higher average PP with flood than with ebb flow (t = 2.54, p = 0.026, n = 10; Table 2).

In general, tidal flux had no significant influence on diatom and dinoflagellate abundance during the 1999 and 2000 samplings. In June 1999 and June 2000, average abundance of diatoms and dinoflagellates had no significant differences with tidal flux or location (Table 3; two-way ANOVA, p >0.05), but in some cases the average and standard error values for dinoflagellate abundance were much larger than those for the other samplings (i.e., the June 1999 FB1 and the June 2000 FB3 values). In April 2000, diatoms were the dominant group at both FB1 and FB2. In April and June 2000, diatoms were more represented at FB1 than at FB2. Opposite to diatoms, dinoflagellates had no significant differences with location. The large standard errors indicate the patchy distribution of these phytoplankton groups (Table 3). During the June-July 1979 sampling, average of diatom abundance was higher at FB1' than at FB3' (t = 1.98, p <0.01), while dinoflagellates had no clear gradient between the outer and the inner part of Falsa Bay. In general, average diatom abundance for the 1979 sampling was not significantly different from those for June 1999 and April 2000 surveys. However, significant lower diatom average abundances were found for June 2000 than those for the other sampling dates, including those for 1979 (t = 2.45, p < 0.01). Unlike diatoms, averages of dinoflagellate abundance between those periods were comparable for the outer and inner part of Falsa Bay (Table 3).

In general, the diatom *Cocconeis* sp. and the dinoflagellate *Prorocentrum* spp. dominated the microphytoplankton assemblages of Falsa Bay during the 1999 and 2000 samplings. Some exceptions occurred when *Navicula* sp. (April 2000), *Thalassiossira sp.* (June 1999) and *Euglena* sp. (June 2000) increased their relative abundance drastically. *Euglena* sp. was particularly present at both the outer and inner part of Falsa Bay. During the June 2000 sampling, several dinoflagellates (e.g., *Lingulodinium polyedrum* (Stein) Dodge*, Ceratium* spp, *Protoperidinium depressum* (Bailey) Balech and diatoms (e.g., *Chaetoceros* spp.) with an oceanic origin were not present at FB2, even though they were a significant part of the microphytoplankton community at FB1 and FB3. As a general observation, more diatom taxa were found at FB2 than at FB1 and FB3, while the opposite was true for dinoflagellates.

Table 1. Averages of vertical PAR attenuation coefficient (K_{PAR}, m^{-1}) and Chlorophyll *a* (Chl-*a*) fractions (mg m^{-3}). In each case, upper row is for ebb flux, lower row is for flood flux. Between parentheses is one standard error. No data were generated for dates with empty spaces.

Date	Site	K_{PAR}	Chl-*a* <10 µm	Chl-*a* %<10 µm	Chl-*a* 10-20 µm	Chl-*a* %10-20 µm	Chl-*a* >20 µm	Chl-*a* %>20 µm
6/15/99	FB2	0.57	1.91	76.0				
		(0.04)	(0.40)					
		0.82	1.33	76.5				
		(0.03)	(0.35)					
4/7/00	FB1	0.80	2.00	56.3				
		(0.22)	(1.28)					
		1.58	0.85	24.6				
		(0.35)	(0.13)					
	FB2	0.67	1.35	71.1				
		(0.15)	(0.30)					
		0.67	0.91	29.0				
		(0.13)	(0.15)					
6/12/00	FB1	0.57	0.39	37.9	0.14	13.6	0.50	48.5
		(0.17)	(0.04)		(0.02)		(0.06)	
		0.50	0.78	43.4	0.23	12.6	0.79	44.0
		(0.08)	(0.02)		(0.05)		(0.11)	
	FB2	0.42	0.37	62.3	0.14	23.1	0.08	14.6
		(0.25)	(0.06)		(0.01)		(0.06)	
		0.58	0.43	43.9	0.46	46.8	0.09	9.3
		(0.33)	(0.02)		(0.04)		(0.05)	
	FB3	0.65	0.81	81.1	0.10	10.4	0.09	8.5
		(0.16)	(0.05)		(0.03)		(0.02)	
		0.73	0.85	73.6	0.14	12.4	0.16	14.0
		(0.28)	(0.02)		(0.02)		(0.02)	

Table 2. Averages of phytoplankton productivity, fractions (mg C m^{-3} h^{-1}) (in the first row units are µm). In each case upper row is for ebb flux, lower row is for flood flux. Between parentheses is one standard error. No data were generated for dates with empty spaces.

Date	Site	<10	%<10	10-20	%10-20	>20	%>20
6/15/99	FB2	6.2	52.6				
		(1.7)					
		5.7	35.5				
		(1.9)					
4/7/00	FB1	8.7	46.9				
		(2.0)					
		6.6	34.9				
		(8.0)					
	FB2	1.8	91.2				
		(0.4)					
		5.7	76.2				
		(3.5)					
6/12/00	FB1	3.6	72.1	1.3	25.9	0.1	2.0
		(1.1)		(0.6)		(0.3)	
		0.7	20.4	1.0	30.9	1.6	48.7
		(0.3)		(0.02)		(0.2)	

Table 3. Averages of phytoplankton and zooplankton abundance, and dominant phytoplankton taxa. Diato: diatom abundance (10^3 cells L^{-1}), Dino: dinoflagellate abundance (10^3 cells L^{-1}), Cop: copepod abundance (orgs L^{-1}), Tin: tintinnid abundance (orgs L^{-1}). Upper row is for ebb flux, lower row is for flood flux. Between parentheses is one standard error. Notice that FB1' and FB3' averages correspond to ten days. No data were generated for dates with empty spaces.

Date	Site	Diato	Dino	Dominant taxa	Cop	Tin
6/15/99	FB1	27 (10)	120 (49)	*Cocconeis* sp., *Euglena* sp., *Nitzschia pacifica* Cupp, *Lingulodinium polyedrum* (Stein) Dodge, *Ceratium furca* (Ehrenberg) Claparede *et* Lachmann	33 (24)	3,310 (1,046)
		47 (25)	128 (50)	Euglena *sp.*, Cocconeis *sp.*, C. furca	160 (45)	1,178 (534)
	FB2	15 (9)	19 (7)	*Cocconeis* sp., *Thalassiossira* sp., *Ceratium fusus* (Ehrenberg) Dujardin	150 (50)	1,166 (75)
		24 (2)	14 (2)	*Cocconeis* sp., *Navicula* sp., *Euglena* sp., *Prorocentrum minimum* (Pavillard) Schiller	60 (20)	408 (13)
4/7/00	FB1	150 (88)	21 (3)	*Navicula* sp., *Thalassiossira* sp., *Chaetoceros* sp., *L. polyedrum* , *Protoperidinium depressum* (Bailey) Balech	30 (10)	1,238 (562)
		199 (19)	32 (4)	*Navicula* sp., *Thalassiossira* sp., *P. minimum,* *Oxyphysis* sp.	30 (10)	770 (70)
	FB2	40 (16)	15 (3)	*Navicula* sp., *Euglena* sp., *Cocconeis* sp., *P. minimum*	13 (7)	1,679 (638)
		52 (21)	20 (5)	*Navicula* sp., *Cocconeis* sp., *Skeletonema* cf. *costatum (Greville) Cleve*, P. *minimum*	10 (10)	2,320 (179)

Table 3. Continuation

6/12/00	FB1	8 (2)	40 (12)	*Cocconeis* sp., *Amphora* sp., *Euglena* sp., *L. polyedrum*, *P. minimum*	60 (22)	1,445 (630)
		44 (15)	61 (7)	*Euglena* sp., *Cocconeis* sp., *P. minimum*, *L. polyedrum*	33 (13)	1,323 (613)
	FB2	1 (1)	33 (9)	*Cocconeis* sp., *Euglena* sp., *P. minimum*	33 (18)	1,774 (237)
		2 (2)	77 (32)	*Cocconeis* sp., *Euglena* sp., *N. pacifica*, *P. minimum*, *L. polyedrum*	25 (18)	1,547 (1,088)
	FB3	10 (5)	31 (18)	*Euglena* sp., *Cocconeis* sp., *N. pacifica*, *Prorocentrum micans* Ehrenberg, *L. polyedum*	67 (33)	2,856 (1,172)
		39 (3)	161 (62)	*Euglena* sp., *Cocconeis* sp., *L. polyedrum*	87 (15)	3,063 (1,078)
6/25-7/5 1979	FB1′	90 (18)	23 (5)			
		207 (69)	38 (10)			
	FB3′	25 (3)	12 (2)			
		27 (2)	19 (03)			

On 15-16 June 1999, copepod nauplii average abundance did not show a relation with tidal flux ($p > 0.05$). On the other hand, loricate tintinnids average abundance was higher with ebb flow than with flood flow at FB2 ($t = 3.18$, $p < 0.05$; Table 3). Tidal flow influence on grazer's densities was not significant in April and June 2000. There were no significant differences of the average abundance of grazers between locations. The large standard error is indicative of the patchy distribution of these phytoplankton grazers. Tintinnids were always much more abundant than copepods (Table 3).

DISCUSSION

Aquaculture in Bahía San Quintín is basically restricted to the shoals of Falsa Bay. It started in 1973 with experimental cultures of *C. gigas*, and it was very limited and with little production during the rest of that decade, but commercial production of *C. gigas* increased from 100 to 900 tons year^{-1} during the 1980s, and remained about constant during the 1990s. The intensively cultivated area (~30 oysters m^{-2}) occupied only ~7% of Falsa Bay. This oyster production gives an estimated average of 110 gr m^{-2} for the inner half of Falsa Bay. García-Esquivel *et al.* (2004) estimated a maximum carrying capacity of this area oscillating between ~2,000 and ~6,000 tons based on determinations of seston, water renewal, and the ingestion rate of oysters.

Unfortunately, there has been no proper monitoring of the phytoplankton composition, biomass, abundance and PP for any site of Bahía San Quintín. Thus, it is not possible to have a robust assessment of the effect of oyster culture on the phytoplankton community of this bay. Nevertheless, as a first approximation, comparing our scarce results with the also scarce data of Millán-Núñez *et al*. (1982), we cannot support the hypothesis that the phytoplankton biomass, abundance and PP have decreased significantly after ~20 years of *C. gigas* commercial cultures. The statistical tests do not allow for rejection of the null hypothesis. It may be argued that one-day samplings do not properly represent the average of these water properties. However, results from Millán-Núñez *et al*. (1982) show that at the inner reaches of Bahía San Quintín the day-to-day averages do not change significantly during few days (10 days) and this supports the validity of averages from every-hour one-day samplings. Horizontal chl-*a*, microphytoplankton abundance and PP distributions throughout Falsa Bay, and changes with tidal flow, were similar for 25 June - 5 July 1979, 15-16 June 1999 and 7 April 2000. Differences in the comparisons of chl-*a*, phytoplankton abundance, and PP between 1979 and 1999-2000 (Figs. 2, 3 and 4) may be due to the fact that chl-*a* determinations may miss part of the picoplankton fraction. The phytoplankton abundance data missed all nanno- and picophytoplankton, while total PP includes all phytoplankton fractions.

Unlike this study, Souchu *et al*. (2001) found important and steady chl-*a* deficits (up to 44%) over areas cultivated with *C. gigas* in the Mediterranean Thau lagoon. Lower oyster density and much shorter water residence time (~8 days, Monreal-Gómez, 1980) in Falsa Bay compared to those of Thau lagoon might explain the differences between the chl-*a* behavior of these two coastal bodies.

Since the early studies of the chl-*a* spatial distribution in Bahía San Quintín, it has been reported that during spring and summer (the intense upwelling events season) chl-*a* decreases from the lagoon's entrance to the inner reaches. At the heads of the lagoon, phytoplankton abundance is ten-fold lower, productivity and chl-*a* are three-fold lower, average chlorophyll content per cell is three-fold higher, and turbidity is higher than at the mouth (Alvarez-Borrego, 2004). The data of Millán-Núñez *et al.* (1982) show that most of these gradients occur in the region between the lagoon's mouth and the base of the "Y" (FB1'). But occasionally some of the change may be detected for the region between the entrance and the inner reaches of Falsa Bay (e.g., between FB1 and FB2), as it is shown by the PP average values for June-July, 1979, and for April 2000 (Fig. 4). Zooplankton grazing does not seem to be the cause of differences between locations. Considering a clearance rate of 0.75 µl h^{-1} tintinnid^{-1} (Christoffersen & Gonzalez, 2003) and a mean tintinnid abundance of $2{\cdot}10^{3}$ orgs l^{-1}, chl-*a* depletion due to these ciliates appears to be negligible (~0.003% per day). Therefore, environmental factors, such as larger turbidity, might be the cause of lower PP for the inner part of Falsa Bay, for both 1979 and 2000. Alvarez-Borrego (2004) hypothesized that differences in iron availability may cause PP to decrease from the lagoon's mouth to the inner reaches of Bahía San Quintín during an upwelling event.

The June 2000 chl-*a* averages were significantly lower than those for June-July 1979, and for the other two of our samplings, for both locations in Falsa Bay. The effect of oysters may not be the explanation for this phytoplankton decline since chl-*a* was relatively high in June 1999, when *C. gigas* production was 20% higher than that of 2000. An alternative mechanism to explain the relatively low June 2000 chl-*a* average values could be related to climate forcing differences between the sampling periods of 1979, 1999 and 2000. Upwelling intensities, expressed as Bakun Index values (m^{3} s^{-1}10^{-2} m^{-1}), calculated for June of 2000 (UI = 70) were lower than those for June 1979 (UI = 234), June 1999 (UI = 121), and April 2000 (UI = 114). Stronger upwelling events off California and Baja California increase phytoplankton growth and this has an impact inside Bahía San Quintín due to transport by tidal currents (Alvarez-Borrego, 2004). Thus, differences in chl-*a* values between samplings seem to be due to environmental changes and not to the oysters under culture.

The diatom and dinoflagellate spatial distributions for 1999 and 2000 remained similar to those of 1979. Diatom abundances lower than those of 25 June - 5 July 1979 were found only for 12 June 2000 (Table 3) and, as it is discussed above, this phenomenon could be associated with lower upwelling intensities during June 2000. Our phytoplankton abundance data only include those cells >5 µm. Thus, we cannot rule out a potential effect of oyster filter-feeding activity on smaller fractions, such as that of microflagellates (members of nannoplankton). In general, our chl-*a* and PP fraction data for 1999 and 2000 suggest no effect of oysters on phytoplankton <10 µm. Thus, there seems to be no significant modification of the original microflagellate abundance by *C. gigas*. Under controlled conditions, Dupuy *et al*. (2000) observed that *C. gigas* filtering efficiency decreases with particles <5 µm, and becomes null for picoparticles (<1 µm) since picophytoplankton does not represent a trophic resource for this particular oyster.

In general, benthic diatoms (e.g. *Cocconeis* sp., *Navicula* spp., *Nitzschia* sp.) were the dominant microphytoplankton of the waters of Falsa Bay (oyster and non-oyster areas). These diatoms originate from the top layer of the sediment (Hernández-Becerril & Alvarez-Borrego, 1983) and from the surface of seagrass leaves (Siqueiros-Beltrones & Ibarra-Obando, 1985), and they are transported to the water column by resuspension. Cognie *et al*. (2001) showed selective modifications of benthic diatom structure due to *C. gigas* feeding. However, unlike this work, the observations of Cognie *et al*. (2001) were performed using a flow-through system which can not represent the complex circulation existing naturally in a lagoon like Bahía San Quintín, where water renewal is much stronger.

The phytoplankton biomass (represented by chl-*a* as a proxy) and PP of Bahia San Quintín seems to be still controlled by natural factors acting with a broad range of scales (hourly to multi-annual). In contrast, other estuaries (e.g., Thau lagoon) are more sensitive to shellfish farming due to a lower water renovation (high flushing time) and greater oyster densities. When analyzing decadal variability, this study was not biased by large scale meteorological episodes since the years compared (1979, 1999, and 2000) coincided with non-El Niño conditions. There are plans to increase the present culture gear at Falsa Bay to ~7 fold (García-Esquivel *et al*., 2004). Future studies should focus on the potential impact of new emplacements of *C. gigas* cultures on the phytoplankton community of Falsa Bay.

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