

# Phytoplankton Biomass, Cell Diameter, and Species Composition in the Low Salinity Zone of Northern San Francisco Bay Estuary

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**ABSTRACT:** Phytoplankton chlorophyll *a* concentration, biovolume, cell diameter, and species composition differed across the narrow, low salinity zone between 0.6‰ to 4‰ and may influence copepod food availability in the northern San Francisco Bay Estuary. The highest chlorophyll *a* concentrations (range 3.2–12.3  $\mu\text{g l}^{-1}$ ), widest cell diameters ( $> 5 \mu\text{m}$  diam), highest diatom densities and highest production rates of  $> 10 \mu\text{m}$  diam cells occurred at the landward edge of the salinity zone in April during a strong spring tide and May during a strong neap tide. Near optimum predator/prey ratios, large prey estimated spherical diameters, and high chlorophyll *a* concentrations suggest these phytoplankton communities provided good food quantity and quality for the most abundant copepods, *Eurytemora affinis*, *Sinocalanus doerrii*, and *Pseudodiaptomus forbesi*. At the center of the zone, chlorophyll *a* concentrations, diatom densities, and production rates of  $> 10 \mu\text{m}$  diam cells were lower and cell diameters were smaller than upstream. Downstream transport was accompanied by accumulation of phytoplankton with depth and tide; maximum biomass occurred on spring tide. The lowest chlorophyll *a* concentrations (1.4–3.6  $\mu\text{g l}^{-1}$ ) and consistently high densities (3,000–4,000 cells  $\text{ml}^{-1}$ ) of  $< 5 \mu\text{m}$  diam cells occurred at the seaward edge of the zone, where the green alga *Nannochloris* spp. and the bluegreen alga *Synechococcus* spp. were the most abundant phytoplankton. Low chlorophyll *a* concentrations and production rates of  $> 10 \mu\text{m}$  diam cells, small prey estimated spherical diameters, and high predator/prey ratios suggested the seaward edge of the zone had poor phytoplankton food for copepodids and adult copepods. The seaward decrease in phytoplankton chlorophyll *a* concentration and cell diameter and shift in species composition in the low salinity zone were probably a function of an estuary-wide decrease in chlorophyll *a* concentration, cell diameter, and diatom density since the early 1980s that was enhanced in the low salinity zone by clam herbivory after 1987.

## Introduction

The high chlorophyll *a* (chl *a*) concentration and density of large diatoms in the low salinity zone (LSZ) between 0.6‰ and 4‰ were considered important for estuarine food web production in San Francisco Bay Estuary (SFBE) (Arthur and Ball 1979). The location of the center of the LSZ in Suisun Bay during the spring in the 1970s coincided with high chl *a* concentration and high densities of large diatoms, like *Skeletonema costatum*, *Coscinodiscus* spp., and *Cyclotella* spp. (Arthur and Ball 1979; Ball and Arthur 1979; Cloern 1979; Wong and Cloern 1981; Cloern et al. 1983). High chl *a* concentrations at the center of the zone were hypothesized to be a function of accumulation by a gravitational circulation cell (Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983) and aggregation of  $< 10 \mu\text{m}$  diam freshwater phytoplankton cells exposed to brackish water (Arthur and Ball 1979; Ball and Arthur 1979).

Because it supported zooplankton production needed for larvae, accumulation of phytoplankton biomass in the LSZ was considered to be a primary

factor controlling the interannual variation of fish populations that use Suisun Bay (Arthur and Ball 1979). The link between production in Suisun Bay and fishery resources was supported by statistical analyses which demonstrated a density maximum for many organisms in the food web when the center of the LSZ (2‰) was located in Suisun Bay (Jassby et al. 1995) and a correlation between chl *a* concentration and zooplankton density (Kimmerer et al. 1994; Kimmerer and Orsi 1996; Orsi and Mecum 1996) or biomass (Lehman 1992).

Decreased chl *a* concentration and shifts in species composition since the early 1980s throughout the estuary (Lehman and Smith 1991; Lehman 1992, 1996a) and the factor of 10 decrease in chl *a* concentration in Suisun Bay since 1986 associated with the introduction of the Asian clam *Potamocorbula amurensis* (Nichols et al. 1990; Alpine and Cloern 1992) have raised questions on the ability of the current phytoplankton production in the LSZ to support zooplankton production. Phytoplankton biomass and species composition in the LSZ could still be important for zooplankton in the Suisun Bay region, because alternate food sources are few. Bacteria have lower rates of production

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and are less abundant in the LSZ than upstream during the spring (Hollibaugh and Wong 1999). Their attachment to particles in the LSZ may increase their availability as food. Rotifers are not abundant (Obrebski et al. 1992) and microzooplankton that commonly link the bacterial food source to the macro-zooplankton and meso-zooplankton are not abundant upstream (Ambler et al. 1985). Dilution grazing studies suggest that they may not be as important to the carbon transfer in the food web upstream compared with downstream (Murrell and Hollibaugh 1998). Chl *a* concentration can reach pre-clam levels in wet years (Lehman 1996b) and diatoms are still the primary food found in the gut of copepods (Orsi 1995). The relative spatial and temporal importance of phytoplankton to the food web is unknown.

Research in other estuaries has demonstrated strong spatial and temporal variation in phytoplankton biomass, species composition, and cell diameter across a narrow salinity zone like that in SFBE. Longitudinal gradients often characterize chl *a* concentrations in rivers, where concentrations increase on ebb tide when phytoplankton are transported downstream (Malone 1977; Lafleur et al. 1979; Demers et al. 1986; Dustan and Pickney 1989); and during neap tide, when upstream phytoplankton are transported downstream and mixing is reduced (Sinclair 1978; Lafleur et al. 1979; Seliger et al. 1981; Le Fevre 1986). In south San Francisco Bay, chl *a* concentrations were higher on ebb tide (Cloern et al. 1989). Frontal zones created by the convergence of seaward river flow and landward tidal flow can also concentrate phytoplankton biomass at the center of the salinity gradient in rivers (Dustan and Pickney 1989) and along the coast (Le Fevre 1986).

In a similar fashion, species composition varies along the longitudinal axis of estuaries in response to riverine transport and mixing associated with ebb-flood asymmetry and causes an increase in freshwater species downstream on ebb tide (Sinclair et al. 1980; Lafleur et al. 1979; Frenette et al. 1995). Changes in species composition caused by downstream transport (Sinclair 1978; Lafleur et al. 1979; Sinclair et al. 1980; Frenette et al. 1995) and mixing (Levasseur et al. 1984; Demers et al. 1986; Turpin and Harrison 1980) also influence the size structure of the phytoplankton community along the gradient. In addition, sedimentation and re-suspension create vertical structure along a salinity gradient by increasing biomass and large diameter cells near the bottom (Frenette et al. 1995) where they may be trapped by horizontal salinity shear (Therriault et al. 1990).

This study characterizes the intertidal spatial and temporal variation of phytoplankton chl *a* concen-

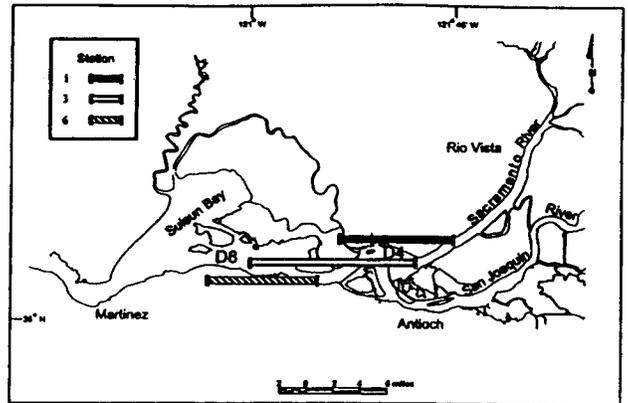


Fig. 1. Map of the sampling area depicting the geographical range of salinity stations in Suisun Bay, the northern reach of San Francisco Bay, and the Sacramento River, part of the Sacramento-San Joaquin River Delta.

tration, cell diameter, and species composition in the 0.6–4‰ LSZ during the spring, determines if the characteristics of the phytoplankton community in the LSZ have changed over time, and qualitatively assesses the quantity and quality of phytoplankton food available to copepods in the LSZ. This information can be used to assist evaluation of the current estuarine management strategy to enhance production by positioning the LSZ in Suisun Bay during the spring.

#### Methods

Phytoplankton and zooplankton were collected at 1-m, 5-m, and 10-m depths for a full tidal cycle (30 h) during a strong spring tide on April 27–28, 1994 and a strong neap tide on May 17–18, 1994. Water samples for phytoplankton and zooplankton were collected using a submersible pump (100 l min<sup>-1</sup>) as the sampling boat moved from the specific conductance of 1 mS cm<sup>-1</sup> to 3 mS cm<sup>-1</sup> and then to 6 mS cm<sup>-1</sup> (hereafter stations 1, 3, and 6, respectively) and back again (Fig. 1). These specific conductance values are equivalent to salinity of 0.6‰, 2‰, and 4‰, respectively, based on salinity conversion equations that include corrections for water-year type and location (K. Guivetchi, unpublished data). The Lagrangian sampling scheme enabled samples to be collected at ebb, flood, and slack tide at station 3 and at ebb and flood tide at stations 1 and 6. More samples were collected at the 2‰ station because it was hypothesized to be an important location for aquatic production in the San Francisco Bay estuary. Additional samples collected along the longitudinal axis of the estuary by a second boat provided information on the phytoplankton communities upstream and downstream of the LSZ.

Replicate water samples for chl *a* measurement were filtered onto 0.4- $\mu\text{m}$  pore size GF/C glass fiber filters, which were neutralized with magnesium carbonate and frozen until analysis. Chl *a* was extracted using a mixture of acetone, dimethyl sulfoxide (DMSO), and water in a ratio of 9:9:2. Concentrations were calculated from fluorescence on a Turner Designs model 10 fluorometer using equations derived from Strickland and Parsons (1972). Total chl *a* concentration was measured at all stations. In addition, chl *a* concentrations in ultraplankton (< 5  $\mu\text{m}$ ), nanoplankton (5–20  $\mu\text{m}$ ), and microplankton (> 20  $\mu\text{m}$ ) size fractions were measured at station 3. Chl *a* concentrations in the < 5  $\mu\text{m}$  and < 20  $\mu\text{m}$  size fractions were determined from filtrate collected after passing the water sample through a 5  $\mu\text{m}$  or 20  $\mu\text{m}$  nitex sieve. Concentrations in the 5–20  $\mu\text{m}$  and > 20  $\mu\text{m}$  size fractions were determined by subtraction.

Phytoplankton species composition, density, and cell dimensions were determined from 50-ml water samples preserved with Lugol's solution and analyzed using the Utermöhl (1958) inverted microscope technique, at 1250 $\times$  magnification. Phytoplankton was categorized as microplankton, nanoplankton, or ultraplankton, using cell diameters and the same size categories used for chl *a* size fractions. Phytoplankton species were divided into groups: diatom, green algae, chrysophyte, cryptophyte, bluegreen algae, dinoflagellate, green flagellate, and miscellaneous flagellate (Lehman 1996a). Biovolumes ( $\mu\text{m}^3$ ) were calculated using measured cell dimensions applied to simple geometrical shapes and corrected for the large vacuole in diatoms (Strathmann 1967). This correction made the biovolume data a surrogate for cell biomass.

Zooplankton water samples were passed from the submersible pump through a 20-cm diam non-collapsible hose into a zooplankton net (35 mesh). No adverse effect of the pumping system was observed on the zooplankton. Zooplankton collected in the cod end of the net were immediately preserved in 2–5% formalin and were sorted and identified to species using a dissecting microscope.

The optimum size phytoplankton food for copepods was estimated using equivalent spherical diameters (ESD) for phytoplankton and zooplankton and predator to prey ratios that were calculated as the ESD for copepods divided by the ESD for phytoplankton cells collected simultaneously (Hansen et al. 1994). Equivalent spherical diameters were determined for phytoplankton from biovolumes and for copepods from dry weight conversions to volume using the equations of McCauley (1984). Dry weights for SFBE copepod species were obtained from J. Orsi (unpublished data).

Phytoplankton and zooplankton production rates were estimated from calculated values. The estimated phytoplankton production rate of > 10  $\mu\text{m}$  diam cells was calculated using estimates of cell carbon based on corrected biovolume (Strathmann 1967) and a carbon to chlorophyll ratio of 50 (Jassby and Powell 1994). Estimated zooplankton carbon was calculated from dry weight estimates multiplied by 0.45 (Hansen et al. 1994). Copepod growth rates were estimated at 0.10  $\text{d}^{-1}$  for adults and 0.27  $\text{d}^{-1}$  for juveniles (Peterson et al. 1991).

Tidal velocities were measured at each station using an acoustic Doppler Continuous Profiler (ADCP) attached to the side of the ship. Velocities ( $\text{cm s}^{-1}$ ) were measured at 0.25-m intervals from the bottom and averaged over the depths at which samples were taken.

Long-term monitoring data used for comparison with data in this study were obtained from the Interagency Ecological Program data files of the California Department of Water Resources (CDWR) and U.S. Bureau of Reclamation (USBR) for stations D4 (RSAC084) and D8 (RSAC068) and California Department of Fish and Game (CDFG) for stations RSAC059 through RSAC095.

Nonparametric statistics were used to analyze most of the data and included single ( $\chi^2$ ) and multiple (Kruskal-Wallis) comparison tests, correlation (Spearman), and linear trend analyses (Kendall Tau b). All statistical analyses were done using Statistical Analysis System (SAS) software (SAS Institute Inc. 1989).

## Results

### PHYTOPLANKTON BIOMASS

The highest phytoplankton biomass occurred at the landward edge of the LSZ and decreased seaward during both spring and neap tide. Median chl *a* concentration decreased seaward from 4.5–9  $\mu\text{g l}^{-1}$  at station 1 (range 3.2–12.3  $\mu\text{g l}^{-1}$ ) to 2.4–2.5  $\mu\text{g l}^{-1}$  (range 1.45–3.6  $\mu\text{g l}^{-1}$ ) at station 6 (Fig. 2). Concentrations were not statistically different between stations 3 and 6, which both had significantly lower ( $p < 0.05$ ) concentrations than station 1. These chl *a* concentrations were similar to those measured between 1970 and 1993 at station 1, but were at most half of those previously measured at station 6 (Figs. 2 and 3). Concentrations at station 3 were similar to those measured previously during spring tide, but were lower during neap tide.

The seaward decrease in chl *a* concentration across the LSZ was accompanied by increased concentrations with depth and tide. At station 3, concentrations were up to 30% higher ( $p < 0.05$ ) at mid-depth and bottom during spring tide and at

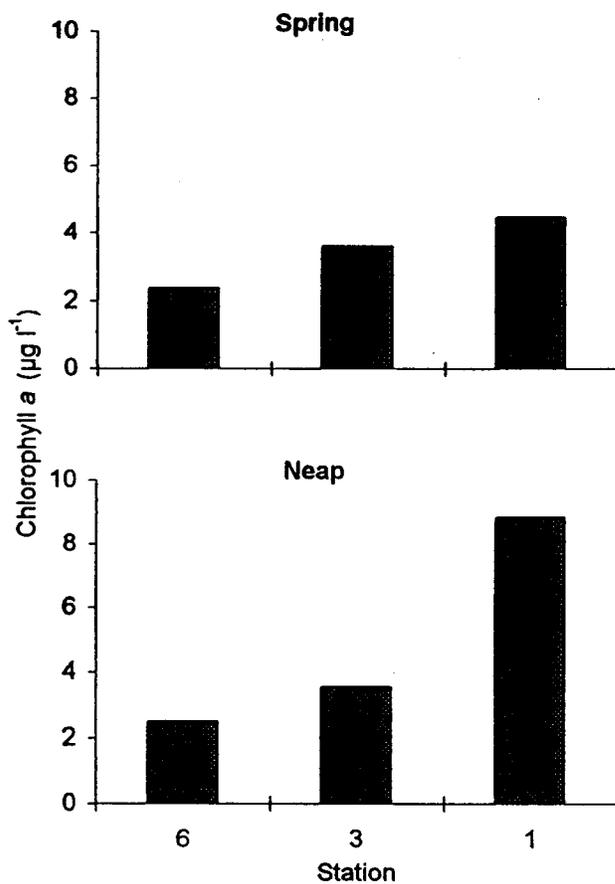


Fig. 2. Median chlorophyll *a* concentrations at stations 6, 3, and 1 across the low salinity zone during spring and neap tide.

the bottom during neap tide (Fig. 4). At station 6, bottom concentrations were again up to 30% higher during spring tide ( $p < 0.05$ ) and tended to be higher during neap tide. Reduced tidal velocity with depth may have contributed to higher chl *a* concentration near the bottom at station 3. Here regression coefficients ( $r^2$ ) between chl *a* concentration and tidal velocity were highest at the surface and decreased with depth for both spring and neap tide (Table 1). This would have allowed settling near the bottom regardless of the difference in direction of flow between spring and neap tide indicated by the opposite sign of the regression slopes. Daily tide further concentrated chl *a* at the center of the LSZ, where concentrations were up to three times higher ( $p < 0.05$ ) on maximum flood during spring tide and on maximum ebb during neap tide (Fig. 5).

#### PHYTOPLANKTON SIZE STRUCTURE

The seaward decrease in chl *a* concentration was accompanied by a decrease in phytoplankton cell diameter. During spring tide, median cell diameter

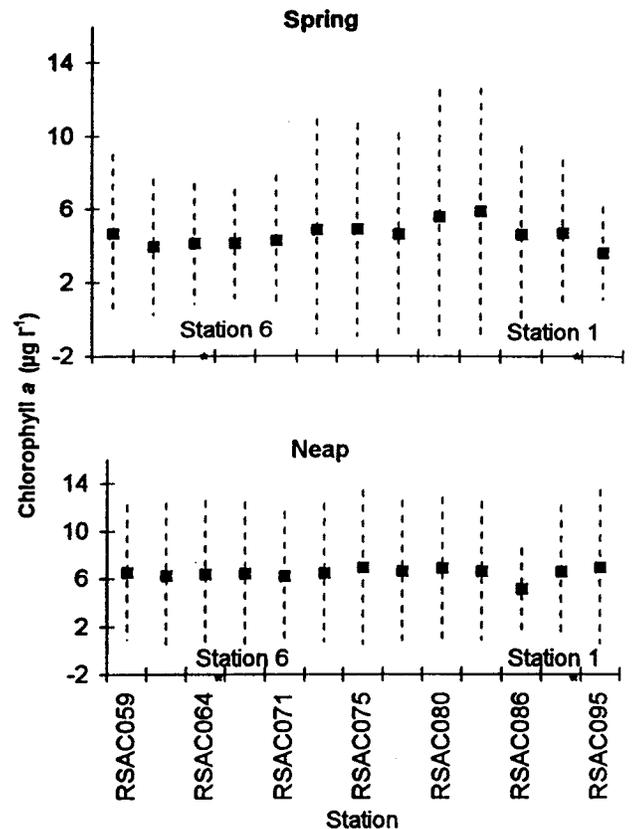


Fig. 3. Mean and standard deviation of chlorophyll *a* concentrations measured between 1970 and 1993 at long-term monitoring stations corresponding to the section of the channel between stations 6 and 1.

in the LSZ was highest ( $p < 0.05$ ) at station 1, which contained 45% of the microplankton (Fig. 6) and smallest ( $p < 0.05$ ) at station 6, which contained 40% of the ultraplankton. During neap tide, median cell diameter was also significantly higher ( $p < 0.05$ ) at station 1, which contained 50% of the microplankton in the LSZ, and decreased seaward ( $p < 0.05$ ). Nanoplankton and ultraplankton were not significantly different among stations during neap tide.

The high percentage of nanoplankton and ultraplankton in 1994 was part of an increase in the number of small diameter cells in the channel after 1983 (Fig. 7). Ratios of 5–20  $\mu\text{m}$  to  $> 20 \mu\text{m}$  diam cells were higher after 1983 ( $p < 0.05$ ) at long-term CDWR monitoring stations D8 (near station 6) and D4 (near station 1) during April and May and increased over time at both stations during spring tide (Kendall Tau  $b$ ,  $p < 0.01$ ). The increase in small diameter cells, however, was probably greater than the long-term monitoring data suggested, because the magnification (750 $\times$ ) used

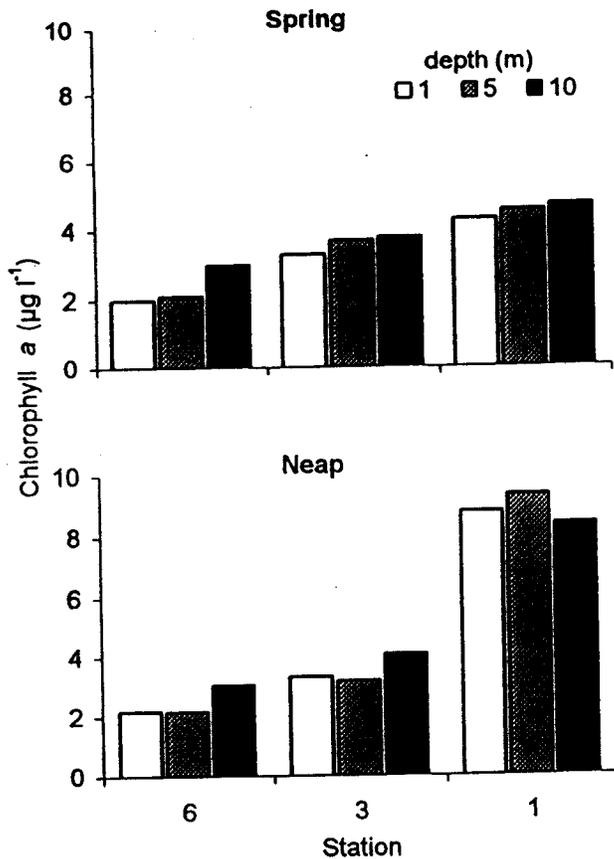


Fig. 4. Median chlorophyll *a* concentration among depths across the low salinity zone during spring and neap tide.

for the monitoring data was too low to quantify < 7 µm diam cells.

Phytoplankton cell diameter also varied with depth and tide at station 3. Based on chl *a* size fraction data, nanoplankton biomass tended to be higher at mid-depth and bottom during spring tide and was significantly higher ( $p < 0.05$ ) at the bottom during neap tide. Ultraplankton biomass was significantly higher ( $p < 0.05$ ) near the surface during neap tide (Fig. 8). Daily tide accumulated microplankton and nanoplankton biomass in a fashion similar to total chl *a* concentration; nanoplankton was significantly higher ( $p < 0.05$ ) on flood during spring tide and both microplankton and nanoplankton were significantly higher ( $p < 0.05$ ) on ebb during neap tide (Fig. 9).

#### PHYTOPLANKTON SPECIES DENSITY AND BIOMASS

A seaward decrease of diatoms and landward increase of green and bluegreen ultraplankton produced the decrease in phytoplankton biomass and cell diameter across the LSZ. During spring tide, diatom density and biomass were highest ( $p <$

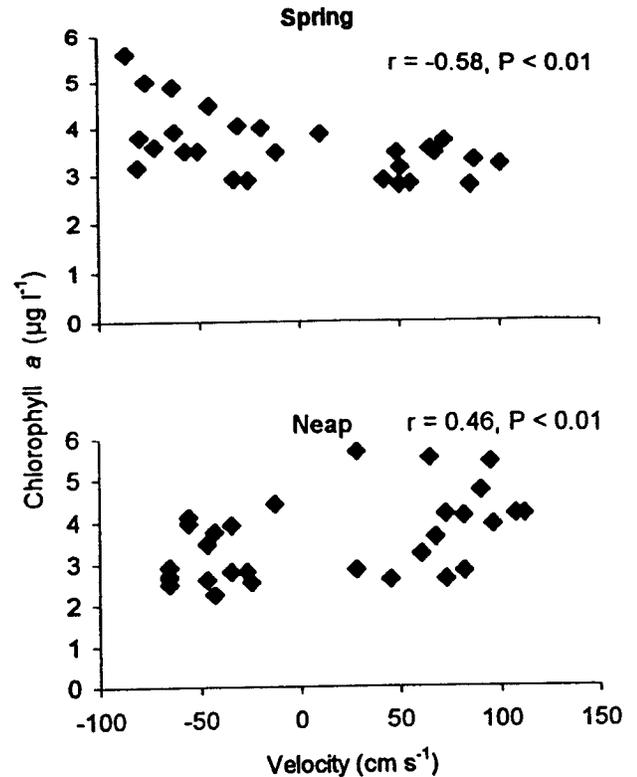


Fig. 5. Regressions of chlorophyll *a* concentration and tidal velocity among depths at station 3 during spring and neap tide.

0.05) at station 1 and decreased seaward (Fig. 10). This contrasted with green algae that were least abundant ( $p < 0.05$ ) at station 1 and increased seaward. Although green algae were abundant at station 6, they comprised no more than 30% of the biomass. During neap tide, diatom density and biomass were also highest ( $p < 0.05$ ) at station 1 and decreased seaward. Green and bluegreen algae were abundant throughout the zone, with more green algae at station 3 and bluegreen algae at station 6, however, green and bluegreen algae combined comprised no more than 30% of the bio volume at all stations.

Only ten species were responsible for the majority of the changes in phytoplankton density and biomass in the LSZ. Among these, the ultraplankton, *Nannochloris* spp. (< 3 µm diam), a green alga and *Synechococcus* spp. (< 2 µm diam), a bluegreen alga, were the most abundant (Fig. 11), reaching densities of 2,000–4,000 cells ml<sup>-1</sup>. The most abundant microplankton and nanoplankton were centric diatoms in the genera *Aulacoseira*, *Coscinodiscus*, *Cyclotella*, and *Thalassiosira*. These genera were far less abundant than green and bluegreen algae; their maximum density reached by *A. granulata* was only 900 cells ml<sup>-1</sup>.

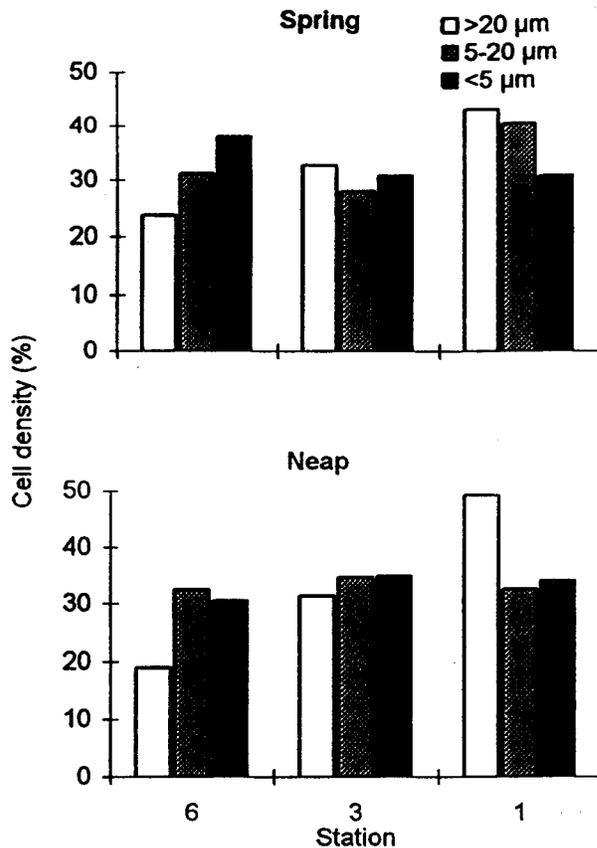


Fig. 6. Percent density of microplankton ( $> 20 \mu\text{m}$ ), nanoplankton ( $5\text{--}20 \mu\text{m}$ ) and ultraplankton ( $< 5 \mu\text{m}$ ) at stations 6, 3, and 1 in the low salinity zone during spring and neap tide.

TABLE 1. Regression statistics for log chlorophyll *a* concentration and tidal velocity measured at station 3 during neap and spring tide.

Depth	df	Intercept	Slope	$r^2$	p
Spring					
1	17	0.63	$-6.53 \times 10^{-4}$	0.37	0.01
5	17	0.67	$-4.50 \times 10^{-4}$	0.31	0.02
10	17	0.67	$-5.42 \times 10^{-4}$	0.24	0.04
All depths	53	0.66	$-5.86 \times 10^{-4}$	0.31	0.00
Neap					
1	17	0.62	$6.36 \times 10^{-4}$	0.22	0.05
5	17	0.60	$5.60 \times 10^{-4}$	0.11	ns
10	17	0.70	$3.27 \times 10^{-4}$	0.06	ns
All depths	53	0.64	$5.69 \times 10^{-4}$	0.12	0.01

The density and biomass of these species demonstrated significant patterns across the LSZ. During spring tide, single-celled diatoms, like *Cyclotella striata* and *Coscinodiscus excentricus* were most abundant ( $p < 0.01$ ) at station 1 (Fig. 11). The chain-forming diatom, *Thalassiosira decipiens*, was also most abundant at station 1, and decreased ( $p < 0.01$ ) seaward. Only the large ( $> 40 \mu\text{m}$  diam) single-celled diatom, *C. lineatus*, was most abundant ( $p < 0.01$ ) at station 6, but it comprised  $< 10\%$  of the biomass. The biovolume and density of the green algae, *Nannochloris* spp. was highest ( $p < 0.01$ ) at station 6 where it comprised 94% of the cells and up to 27% of the biovolume. The phytoplankton community was mixed at the center of the zone.

During neap tide, the large chain-forming diatom, *A. granulata*, was abundant and comprised most of the biomass in the zone (Fig. 11). Density and biovolume were highest at station 1 and decreased ( $p < 0.01$ ) seaward. In contrast, *C. excen-*

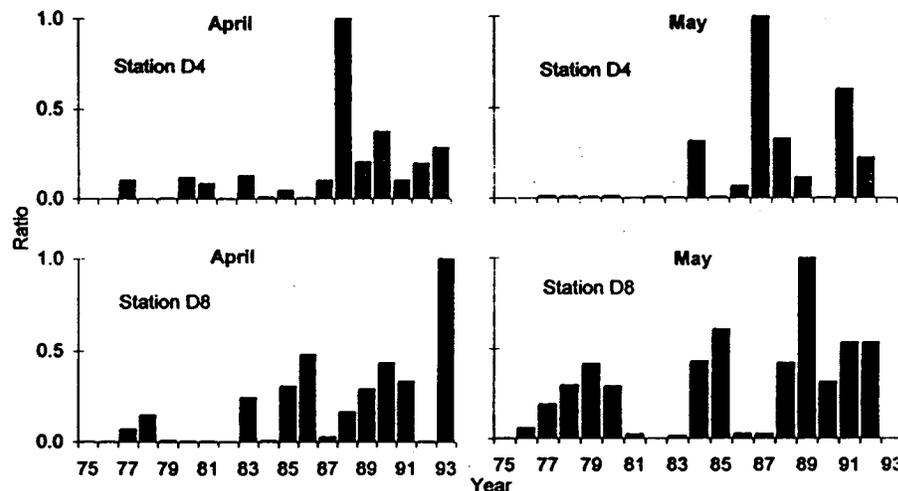


Fig. 7. Ratio of nanoplankton ( $5\text{--}20 \mu\text{m}$ ) to microplankton ( $> 20 \mu\text{m}$ ) cell density at long-term monitoring stations D4 and D8 during April and May between 1970 and 1993.

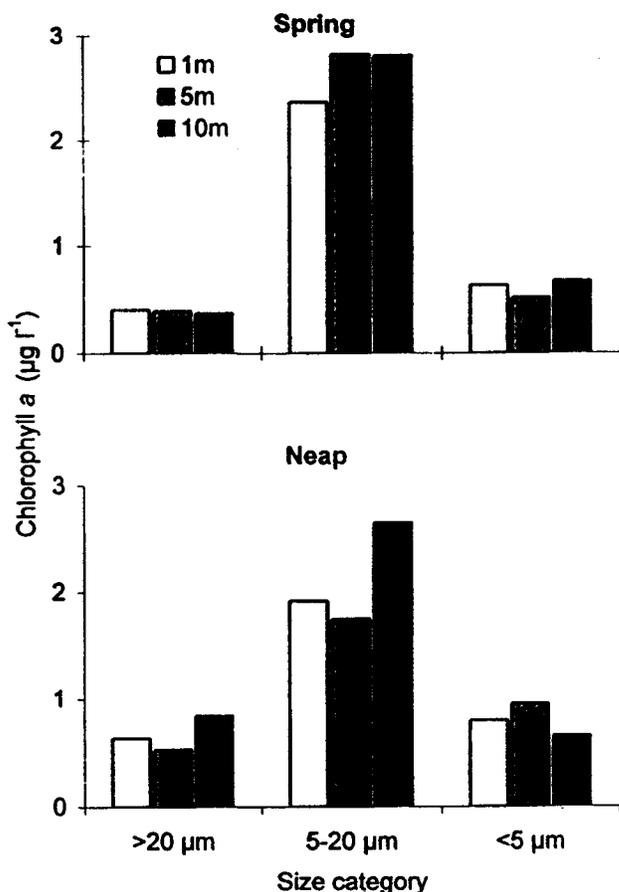


Fig. 8. Chlorophyll *a* concentration in microplankton (> 20  $\mu\text{m}$ ), nanoplankton (5–10  $\mu\text{m}$ ), and ultraplankton (< 5  $\mu\text{m}$ ) size fractions among depths at station 3 during spring and neap tide.

*tricus*, *C. lineatus*, and *C. meneghiniana* density and biovolume tended to be higher at station 6. The green ultraplankton *Nannochloris* spp. was abundant at all stations and was accompanied by the bluegreen ultraplankton *Synechococcus* spp. at station 6.

#### PHYTOPLANKTON AS COPEPOD FOOD

The decrease in phytoplankton biomass, cell diameter, and diatom density across the LSZ could have affected the quantity and quality of phytoplankton food available to copepods in the zone. Chl *a* concentration and total copepod biomass were significantly correlated ( $p < 0.01$ ) and both maximum phytoplankton and copepod biomass occurred at station 1 (Fig. 12). Over 55% of the copepod biomass occurred at the landward edge of the LSZ for each of the most abundant copepods, *Pseudodiaptomus forbesi*, *Sinocalanus doerrii*, and *Eurytemora affinis*, except during spring tide when *E. affinis* biomass was equally distributed be-

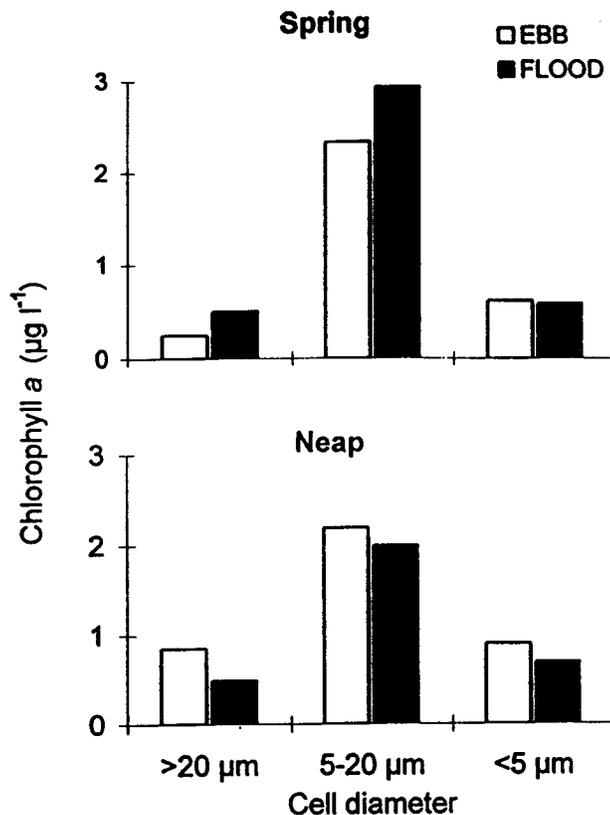


Fig. 9. Chlorophyll *a* concentrations in microplankton (> 20  $\mu\text{m}$ ), nanoplankton (5–10  $\mu\text{m}$ ), and ultraplankton (< 5  $\mu\text{m}$ ) size fractions on ebb and flood tide at station 3 during spring and neap tide.

tween stations 1 and 3 (not shown). Maximum copepod biomass occurred at station 1 despite a shift in species dominance in the LSZ from *E. affinis* during spring tide to *P. forbesi* during neap tide.

A decrease in phytoplankton cell diameter across the LSZ could also have affected the quality of phytoplankton food available to copepods that are size selective feeders. Many phytoplankton cells fell within the preferred ESD size range of 10–43  $\mu\text{m}$  for adults and copepodids (Hansen et al. 1994) at station 1, where at least 45% of the cells were > 10  $\mu\text{m}$  (ESD) (Table 2; Fig. 13), but not at station 6, where only a few percent of the cells had ESD values > 10  $\mu\text{m}$ . Station 3 had cells within the optimum ESD size range during spring tide, but few during neap tide.

These ESD values were reflected in the median predator/prey ratios that were only within the optimum range of 9–33:1 for adult and juvenile copepods (Hansen et al. 1994) at stations 1 and 3 during spring tide (Fig. 14). Aggregation of phytoplankton with depth and tide may have had some effect on the median and range of predator/prey ratios. Median predator/prey ratios at stations

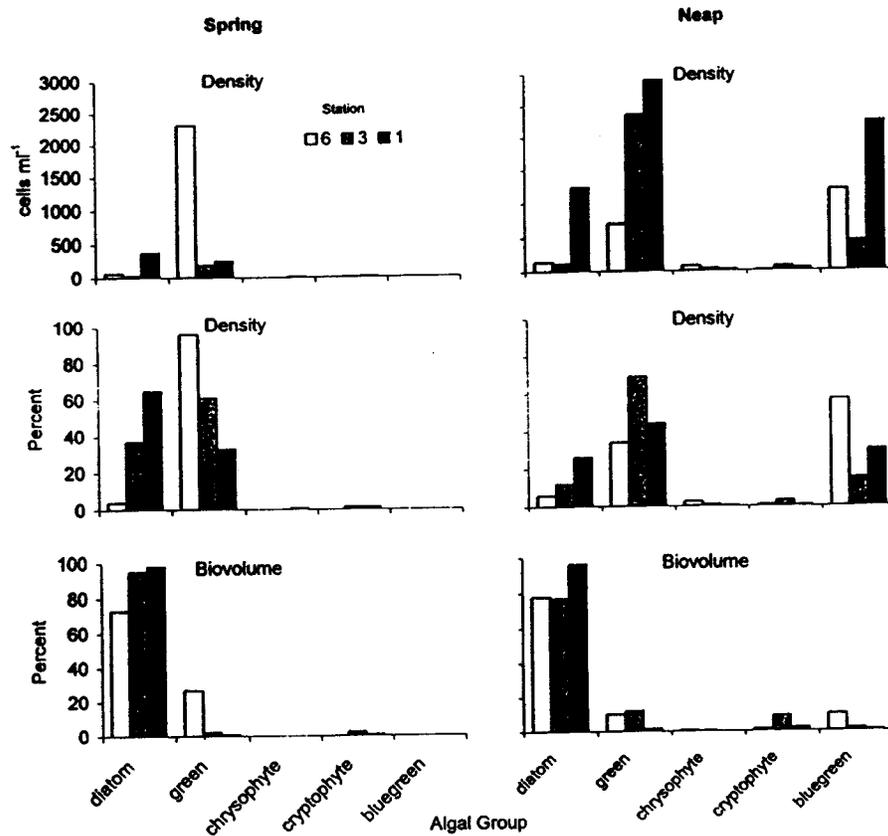


Fig. 10. Density, percent density, and percent biovolume of phytoplankton species groups at stations 6, 3, and 1 in the low salinity zone during spring and neap tide.

1 and 3 were only within the optimum range near the surface and bottom on ebb during spring tide (Table 2; Fig. 14).

The production rate of  $> 10 \mu\text{m}$  diam cells was at least 2 times higher at the landward edge than the seaward edge of the LSZ. The daily estimate of carbon production by these cells supplied less than

10% of the estimated carbon needed for daily copepod growth in the LSZ. Estimated production rates of  $> 10 \mu\text{m}$  diam phytoplankton cells decreased seaward across the LSZ;  $527 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $347 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and  $181 \text{ mg C m}^{-2} \text{ d}^{-1}$  during spring tide and  $484 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $120 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and  $73 \text{ mg C m}^{-2} \text{ d}^{-1}$  during neap tide. The

TABLE 2. Copepod dry weight, carbon and equivalent spherical diameter (ESD), and phytoplankton equivalent spherical diameter needed for optimal predator to prey ratios of selected species.

Species	Dry weight ( $\mu\text{g}$ )		Carbon ( $\mu\text{g}$ )		Volume ( $\mu\text{m}^3$ )		ESD ( $\mu\text{m}$ )		Optimal Phyto ESD ( $\mu\text{m}$ ) Range
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	
<i>Eurytemora affinis</i>									
Female	7.0	5.5–8.5	3.2	2.5–3.8	$2.6 \times 10^7$	$(2.1\text{--}3.2) \times 10^7$	347.7	321.1–370.7	11.6–34.8
Male	5.3	4.5–6.0	2.4	2.0–2.7	$2.0 \times 10^7$	$(1.7\text{--}2.2) \times 10^7$	316.2	300.5–330.5	10.5–31.6
<i>Sinocalanus doerrii</i>									
Female	8.8	7.0–10.5	3.9	3.2–4.7	$3.3 \times 10^7$	$(2.6\text{--}0.4) \times 10^7$	374.3	347.7–397.5	12.4–37.4
Male	6.0	5.0–7.0	2.7	2.2–3.2	$2.3 \times 10^7$	$(1.9\text{--}2.6) \times 10^7$	330.5	311.2–347.7	11.0–33.0
<i>Pseudodiaptomus forbesii</i>									
Female	13.8	13–14.5	6.2	5.8–6.5	$5.2 \times 10^7$	$(4.9\text{--}5.4) \times 10^7$	434.5	426.5–442.2	14.5–43.4
Male	7.4	6.8–8.0	3.3	3.1–3.6	$2.8 \times 10^7$	$(2.6\text{--}3.0) \times 10^7$	354.1	344.4–363.4	11.8–35.4
Copepodids	3.0	—	1.4	—	$1.1 \times 10^7$	—	262.0	—	10.0–29.0
Nauplii	0.3	—	0.1	—	$1.1 \times 10^6$	—	26.2	—	1.0–2.9

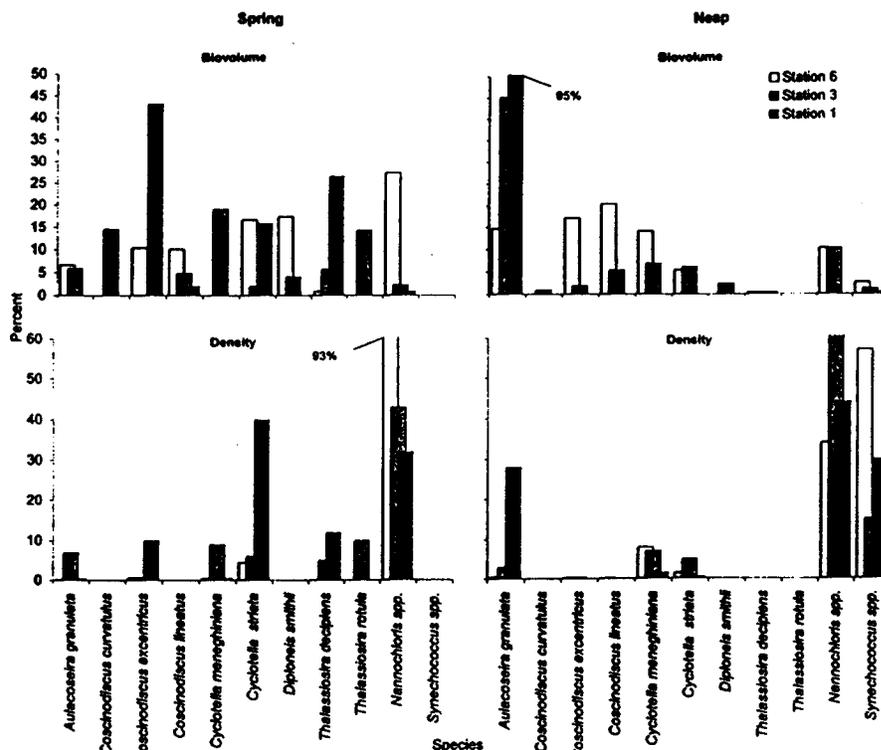


Fig. 11. Percent biovolume and density of phytoplankton species comprising more than 10% of the density or biovolume at stations April 6, 3, and 1 in the low salinity zone during spring and neap tide.

seaward decrease in the estimated production rate of  $>10 \mu\text{m}$  diam phytoplankton cells was accompanied by a seaward decrease in estimated production rates for copepods;  $14,027 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $6,665 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and  $1,687 \text{ mg C m}^{-2} \text{ d}^{-1}$  during spring tide and  $7,042 \text{ mg C m}^{-2} \text{ d}^{-1}$ ,  $1,478 \text{ mg C m}^{-2} \text{ d}^{-1}$ , and  $444 \text{ mg C m}^{-2} \text{ d}^{-1}$  during neap tide.

### Discussion

#### FACTORS INFLUENCING PHYTOPLANKTON ACROSS THE LSZ

Many physical, chemical, and biological factors probably produced the decrease in phytoplankton chl *a* concentration, cell diameter, and diatom density across the LSZ. At the landward edge of the LSZ, the high chl *a* concentrations, large diameter cells, and abundant diatoms were probably transported from upstream phytoplankton communities. Downstream transport, particularly on ebb tide, is an important mechanism controlling chl *a* concentration in estuaries (Malone 1977; Lafleur et al. 1979; Demers et al. 1986; Dustan and Pickney 1989). In South San Francisco Bay, chl *a* concentrations were higher when riverine phytoplankton were transported into the bay on ebb tide (Cloern et al. 1989). That higher chl *a* concentration on ebb tide was produced by upstream phy-

toplankton was corroborated by the increase of diatoms on ebb tide and green and bluegreen algae on flood tide in this study. Freshwater species were also more abundant downstream on ebb tide in the St. Lawrence (Sinclair 1978; Lafleur et al. 1979; Frenette et al. 1995) and Chesapeake Bay (Seliger et al. 1981) estuaries and coastal phytoplankton were more abundant on ebb tide at tidal fronts (Le Fevre 1986).

The lower chl *a* concentrations and diatom densities and smaller diameter cells at the center than at the landward edge of the LSZ were probably due to both dispersion and the loss of freshwater diatoms that lyse (Small et al. 1990) or form aggregates that settle to the bottom in brackish water (Ball and Arthur 1981). Benthic grazing by the clam *P. amurensis* may further contribute to the loss of phytoplankton cells, but its influence is probably less here than downstream, where clam densities are highest. There was no accumulation of phytoplankton biomass or large diameter diatoms, like *Coscinodiscus* spp. or *Skeletonema costatum*, by gravitational circulation as hypothesized previously (Peterson et al. 1975; Arthur and Ball 1979; Cloern et al. 1983). In fact, hydrodynamic measurements taken during this and subsequent studies indicate the salinity gradient in the channel is too small to pro-

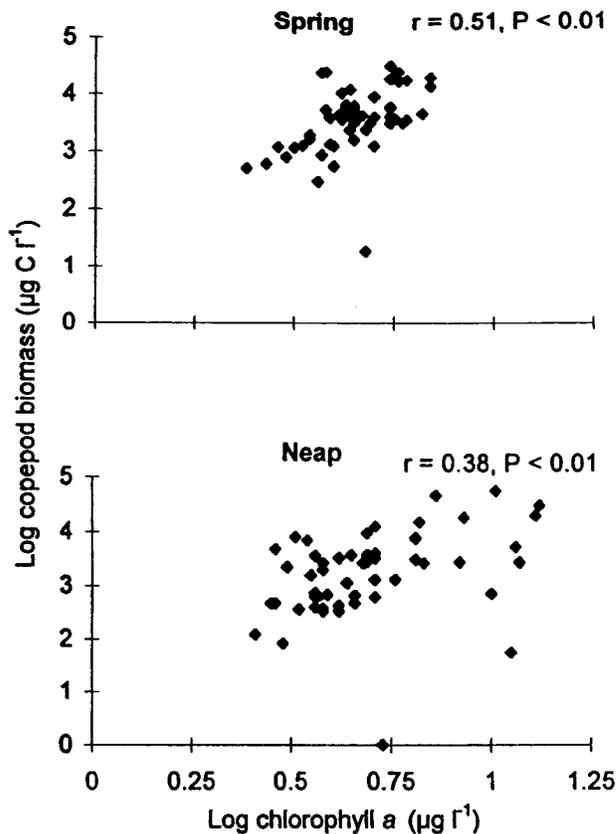


Fig. 12. Correlation between log copepod biomass and log chlorophyll *a* concentration across the low salinity zone during spring and neap tide.

duce gravitational circulation in the spring (Bureau et al. 1998).

Phytoplankton biomass, however, was accumulated with tide at the center of the LSZ. The 3-fold higher chl *a* concentrations on maximum flood during the spring tide could have been produced by local accumulation of phytoplankton at the frontal zone created by the convergence of seaward river flow and landward daily tidal flow, which was magnified by the spring tide (Dustan and Pickney 1989; LeFevre 1986). An opposite process could have produced the 2 times higher chl *a* concentration on maximum ebb during neap tide, when transport of phytoplankton from upstream was enhanced by the seaward flow of both the river and daily tide, magnified this time by the neap tide (Dustan and Pickney 1989). Changes in phytoplankton biomass with ebb-flood or spring-neap asymmetry have often been attributed to riverine transport processes (Sinclair 1978; Lafleur et al. 1979; Seliger et al. 1981; LeFevre 1986; Frenette et al. 1995). Research suggests other potential causes include changes in phytoplankton growth rate due to changes in species composition (Demers et al.

1979; Sinclair et al. 1980) or the influence of mixing on light and nutrient availability (Demers et al. 1986). The latter cause is less likely in SFBE where nutrients are in excess (Lehman 1992).

Tidal flows also influenced cell diameter and species composition at the center of the LSZ, where nanoplankton accumulated during the spring flood and microplankton and nanoplankton accumulated on neap ebb. Strong vertical mixing associated with the spring tide may also have increased nanoplankton cells near the bottom by resuspension, because nanoplankton, the most abundant cells at the bottom, increased during the spring flood. The strong vertical mixing during the spring flood was suggested by the increased height of sediment in the water column and was probably necessary to resuspend cells near the bottom where tidal velocities are lower than near the surface (Bureau et al. 1998). Research has demonstrated changes in phytoplankton species composition and size structure with tide (Sinclair 1978; LaFleur et al. 1979; Sinclair et al. 1980; Frenette et al. 1995) and vertical mixing (Levasseur et al. 1984; Demers et al. 1986; Turpin and Harrison 1980).

At the seaward edge of the LSZ, grazing by the clam *P. amurensis* may be an overriding influence on phytoplankton chl *a* concentration, cell diameter, and species composition. Since its introduction in 1987, the clam has lowered chl *a* concentration in Suisun Bay by a factor of 10 from  $> 20 \mu\text{g l}^{-1}$  to  $< 3 \mu\text{g l}^{-1}$  (Nichols et al. 1990; Alpine and Cloern 1992). Its ability to remove phytoplankton in channels is a function of high densities which reach 6,000 clams  $\text{m}^{-2}$  in drought years (Lehman 1996b), and high grazing rates, that enable it to filter water in 10 m deep channels 1.28 times per day (Werner and Hollibaugh 1993). During April and May 1994, clam densities reached up to 912 clams  $\text{m}^{-2}$  in Suisun Bay and decreased landward (stations D4 and D7; CDWR, unpublished data). The clam may have an equally large effect on phytoplankton cell diameter and species composition. Species identifications at high magnification (1000–1240 $\times$ ) indicate the LSZ had large diameter ( $> 20 \mu\text{m}$ ) marine diatoms in the 1970s (Arthur and Ball 1979; Cloern 1979; Wong and Cloern 1981; Cloern et al. 1983), but small diameter green and bluegreen ultraplankton (1–3  $\mu\text{m}$ ) during this study. The ultraplankton may persist because they are inefficiently grazed by *P. amurensis*, which have poor retention of  $< 5 \mu\text{m}$  diam cells (Werner and Hollibaugh 1993).

The low median chl *a* concentrations at the center and seaward edge of the LSZ were augmented by up to a 30% higher phytoplankton biomass with depth. Higher chl *a* concentration at the bottom was also measured in this region during the 1970s

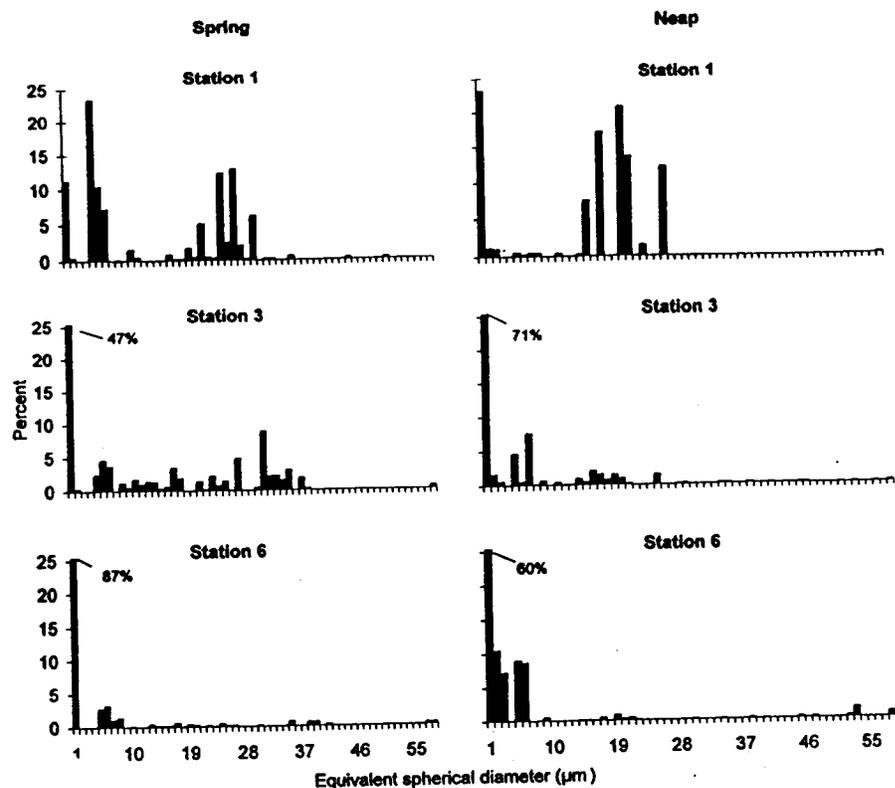


Fig. 13. Percent phytoplankton cells within estimated spherical diameter size categories at stations 6, 3, and 1 during spring and neap tide.

(Arthur and Ball 1979; Ball and Arthur 1979) and was attributed to the high settling rates of 2–6  $\text{m d}^{-1}$  by microplankton and nanoplankton (Ball and Arthur 1981). Most of the cells at the bottom were nanoplankton and the settling of these cells is enhanced by cell aggregations produced when freshwater phytoplankton encounter brackish water (Ball and Arthur 1981).

An increase in biomass at the bottom with distance downstream also occurred in the St. Lawrence Estuary and was attributed to a combination of sedimentation and resuspension (Frenette et al. 1995) and a horizontal salinity shear that traps cells at the bottom (Therriault et al. 1990). These factors may also be important in the LSZ, where settling rates are high, the vertical salinity gradient is small and tidal velocities are reduced near the bottom (Bureau et al. 1998). The increase in chl *a* concentration near the bottom does not contradict the influence of clam grazing on phytoplankton biomass. It is likely that chl *a* concentrations decreased closer to the clam bed than was sampled and that lower filtration rates of clams early in the year, when water temperatures were low (Werner and Hollibaugh 1993) and clams

were small (J. Thompson personal communication), reduced their influence.

#### FOOD WEB IMPLICATIONS

Decreased phytoplankton chl *a* concentration, cell diameter, and diatom density across the LSZ may be important to the SFBE food web, because they may affect the quantity and quality of phytoplankton food available to copepods. Phytoplankton are eaten by copepods (Orsi 1995) and may be an important direct source of copepod food in northern SFBE. Microzooplankton, a common food source for copepods in many estuaries, are less abundant upstream than downstream (Ambler et al. 1985; Murrell and Hollibaugh 1998). Grazing studies suggest they may be less important in the transfer of carbon through the food web upstream than downstream in SFBE (Murrell and Hollibaugh 1998). The relative importance of bacteria, detritus, phytoplankton, and microzooplankton as a food source for copepods in the estuary is unknown.

The high chl *a* concentration at the landward edge of the LSZ suggests phytoplankton food was sufficient for copepod growth and egg production

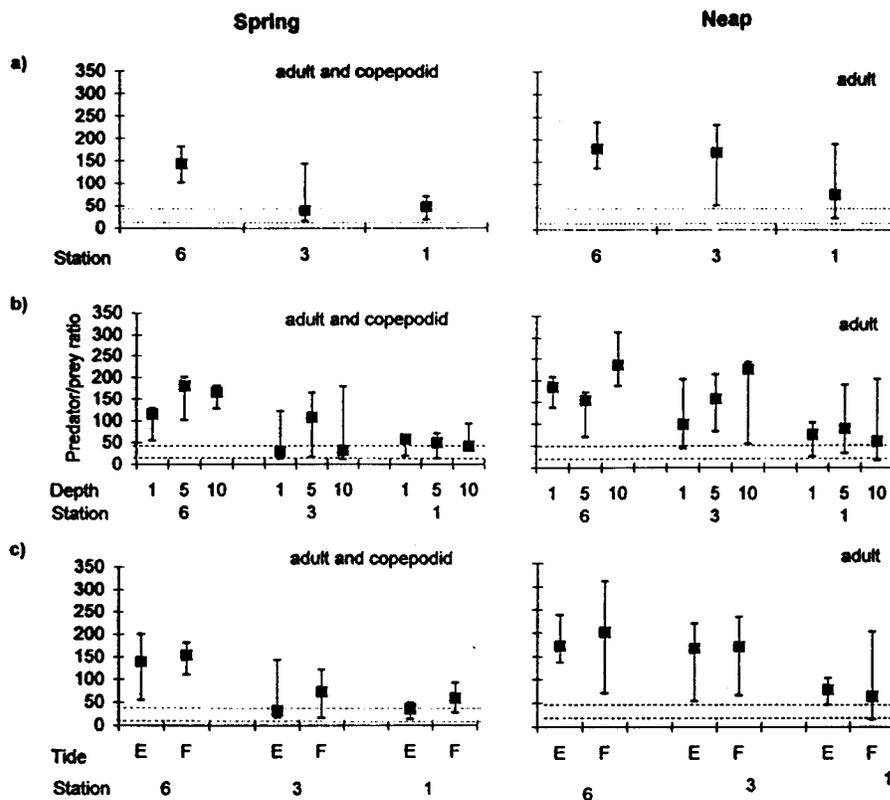


Fig. 14. Median and 5th and 95th percentiles for predator to prey ratios of copepod adults and copepodids at stations 6, 3, and 1 in the low salinity zone during spring and neap tide by a) station, b) depth, and c) ebb (E) and flood (F) tide. No copepodids occurred during neap tide.

because they were above the  $0.5\text{--}2.5\ \mu\text{g l}^{-1}$  threshold concentrations associated with poor growth rate and egg production in copepods (Klein Breteler et al. 1982; Durbin et al. 1983; Kiorboe and Johansen 1986; Berggreen et al. 1988; Kiorboe et al. 1990; Peterson et al. 1991). In contrast, chl *a* concentrations at the seaward edge of the LSZ consistently fell below or near these chl *a* threshold values. Adverse affects of low chl *a* concentration at the center and seaward edge of the LSZ may have been reduced by the increase of phytoplankton biomass with depth and tide because small-scale and periodic increases in phytoplankton biomass can increase food availability for copepods, particularly at tidal fronts where it coincides with peak copepod egg production (Kiorboe and Johansen 1986; Kiorboe et al. 1988).

Chl *a* concentration may not have been the best indicator of phytoplankton food availability in the LSZ, because calanoid copepods are commonly size selective feeders (Hansen et al. 1994) and phytoplankton cell diameter decreased across the LSZ. Phytoplankton food was probably readily available to adult and juvenile copepods at the landward edge of the LSZ where cell diameter between  $8\ \mu\text{m}$

and  $40\ \mu\text{m}$  (Kiorboe et al. 1990; Peterson et al. 1991) and predator/prey ratios between 10 and 30:1 (Hansen et al. 1994) were within the range of optimum values. This range for optimum cell diameter agrees with the cell diameters of phytoplankton found in the guts of *E. affinis* and *S. doerrii* in SFBE (Orsi 1995). As a result, the high percentage of  $< 10\ \mu\text{m}$  ESD cells at the center (60–80%) and seaward edge (95–98%) of the LSZ may have provided poor quality food for juvenile and adult copepods. Production rates of  $> 10\ \mu\text{m}$  diam phytoplankton cells could have compensated only somewhat for the abundance of small diameter cells.

Phytoplankton species composition may have further affected phytoplankton food quality for copepods in the LSZ, but there is no direct information on their effects from this study. Copepods can feed selectively on phytoplankton species (Paffenhofer and Knowles 1978; Peterson et al. 1991; Kiorboe et al. 1990) and the type of phytoplankton eaten can affect molting frequency, growth and mortality rate, and body size (Twombly and Burns 1996). Phytoplankton food quality was probably high at the landward edge of the LSZ where dia-

toms were abundant. Diatoms may be the good quality food for copepods in SFBE where the chain-forming diatoms *Thalassiosira* spp. and *Skeletonema potamos* were the most abundant phytoplankton in the gut of *E. affinis* and *S. doerrii* (Orsi 1995) and the wide cell diameter and large biovolume of diatoms makes them an important source of carbon in the estuary (Lehman 1996a). Even the diatom *A. granulata* which is considered to be poor food, but was abundant in the LSZ, is eaten during non-bloom periods (Orsi 1995) and when chains are short (Fulton 1988). Research in other ecosystems suggests diatoms are less utilized and nutritionally inferior to dinoflagellates as copepod food (Kleppel et al. 1991; Ianora and Poulet 1993). Nevertheless, diatoms comprised most of the optimal sized cells in the LSZ and have been historically abundant in the upper estuary, where dinoflagellates comprise less than 10% of the phytoplankton cells (Lehman 1996b).

#### HISTORICAL PERSPECTIVE

The low chl *a* concentration and diatom density and small cell diameter cells measured in the LSZ was part of a long-term change in the phytoplankton community since the 1970s (Lehman and Smith 1991; Lehman 1992, 1996a,b). The loss of diatoms probably contributed to the decrease in average cell diameter and phytoplankton biomass, because diatoms are the most abundant large diameter cells in the estuary and have a large cell biomass (Lehman 1996a). These changes in phytoplankton biomass and composition were probably caused by a combination of natural and anthropogenic factors and so far have been linked with climate change, water diversions (Lehman and Smith 1991; Jassby and Powell 1994; Lehman 1996a, in press), and benthic grazing (Nichols et al. 1990; Alpine and Cloern 1992). Benthic grazing by the brackish water clam *P. amurensis* was probably a major factor affecting the loss of diatoms at the center and seaward edge of the LSZ, because it is abundant in these brackish waters and would successfully filter diatom cells that are commonly > 5  $\mu\text{m}$  diam (Werner and Hollibaugh 1993).

Although the true diet of copepods in the estuary is unknown, the long-term decrease of phytoplankton biomass, cell diameter, and diatom density in the LSZ may have affected the long-term health of the estuary by contributing to the long-term shifts in copepod species composition. Densities of many large copepods have decreased (Orsi et al. 1983; Orsi and Mecum 1986, 1996; Obrebski et al. 1992) and densities of many introduced species have increased (Orsi et al. 1983; Orsi and Walter 1991) since the early 1970s. None is more important than the decline of the native copepod *E.*

*affinis* that was historically abundant at the center of the zone and has declined since the 1970s (Orsi and Mecum 1986). The sharp decrease of *E. affinis* in the LSZ after introduction of *P. amurensis* in 1987 was due to direct loss to clam filtration (Kimmerer et al. 1994; Kimmerer and Orsi 1996). This study suggests the low chl *a* concentration and diatom density and small cell diameter at the center and landward edge of the LSZ could also have contributed to the loss of this and other native copepods in the region and is another way the clam contributed to the long-term changes in the LSZ food web.

#### Conclusions

Phytoplankton biomass, cell diameter, and diatom density decreased seaward across the LSZ and the amplitude of decrease was dependent on both depth and tide. Because of the changes in the phytoplankton community across the LSZ, phytoplankton at the landward edge of the zone provided the best quantity and quality of phytoplankton food for copepods. The changes in the phytoplankton community across the LSZ were a part of a long-term trend in the estuary caused by a number of natural and anthropogenic factors.

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