Planktonic Properties of Honokohau Harbor: A Nutrient-Enriched Subtropical Embayment[1]

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ABSTRACT: The phytoplankton properties of this nutrient-enriched, vertically stratified harbor show remarkably oligotrophic characteristics considering the eutrophying potential of groundwater nutrient input. Generally, low phytoplankton biomass levels (0.06–0.70 mg chlorophyll a/m^3) and productivity rates (0.30–5.1 mg C/m^3/hr) prevail within the harbor. Zooplankton standing stocks within Honokohau Harbor were highest in the most inland reaches of the basin and showed marked increases (numerically about 28 times and 6 times by dry weight) over levels in adjacent coastal areas. Enteric bacterial (total and fecal coliforms and fecal streptococci) levels were low, despite evidence of sewage leakage into the harbor, reflecting both low input and rapid flushing rates of the basin.

The vertical profiles of phytoplankton parameters reflect the peculiar thermohaline stratification of the water column. Despite high surface nutrient levels, a strongly stratified nutricline apparently limits availability to the subsurface (oceanic) phytoplankton populations. This study discusses the importance of advective removal (via flushing) and grazing in controlling phytoplankton stocks within the basin.

HONOKOHAU HARBOR IS A SUBTROPICAL, vertically stratified embayment with nutrient-rich, brackish surface water overlying a typically nutrient-poor oceanic sublayer. This situation, resulting from the intrusion of groundwater from the island's Ghyben–Herzberg lens through the walls and floor of the inner basin, provides unique growth conditions for the planktonic organisms within the harbor. This paper describes the standing stocks and dynamics of the phytoplankton, zooplankton, and enteric bacterioplankton inhabiting the harbor, with particular reference to the ways in which physical and biological forces act to control these populations. Although various aspects of harbor planktonology were studied over a 5-year period, this report deals mainly with results of a single, intensive survey conducted in February 1975. Details of the water quality characteristics and physical oceanography of

the harbor may be found in Bienfang (1980) and Gallagher (1980), respectively.

MATERIALS AND METHODS

Phytoplankton parameters were measured in the morning and afternoon on 4 days at the nutrient chemistry stations (Bienfang 1980). Stations were located in the inner basin (1), interconnecting channel (2), outer basin (3), entrance channel (4), and about 150 m outside the harbor (5). Phytoplankton standing stocks (chlorophyll a and phaeopigment concentrations) were measured by the extraction/fluorometric method described in Strickland and Parsons (1972). Primary production rates were determined by the C-14 method (Steemann Nielsen 1952) using 4-hr in situ incubation at 0.5, 1.5, and 3.0 m. In addition, a vertical profile of production and biomass was constructed from samples taken at 1-m intervals throughout the 5.5-m water column of the outer basin. Productivity samples were analyzed using a Nuclear Chicago

TABLE 1

Phytoplankton Parameters at Honokohau Harbor, Hawaii

STATION	DEPTH (m)	CHLOROPHYLL *a* FALLING TIDE (AM)	CHLOROPHYLL *a* RISING TIDE (PM)	PHAEOPHYTIN FALLING TIDE (AM)	PHAEOPHYTIN RISING TIDE (PM)	PHAEOPHYTIN/CHLOROPHYLL FALLING TIDE (AM)	PHAEOPHYTIN/CHLOROPHYLL RISING TIDE (PM)	PRIMARY PRODUCTIVITY FALLING TIDE (AM)	PRIMARY PRODUCTIVITY RISING TIDE (PM)	PRODUCTIVITY INDEX FALLING TIDE (AM)	PRODUCTIVITY INDEX RISING TIDE (PM)
1	0.5	0.10 ± 0.01	0.06 ± 0.01	0.11 ± 0.04	0.07 ± 0.01	1.10 ± 0.34	1.17 ± 0.01	0.33	0.58 ± 0.11	3.30 ± 0.33	9.67 ± 0.03
	1.5	0.56 ± 0.24	0.60 ± 0.17	0.36 ± 0.16	0.33 ± 0.34	0.64 ± 0.94	0.55 ± 0.59	3.43 ± 0.06	2.33 ± 0.46	6.13 ± 2.63	3.88 ± 1.61
	3	0.55 ± 0.11	0.70 ± 0.33	0.45 ± 0.27	0.52 ± 0.42	0.82 ± 0.52	0.74 ± 1.26	2.65 ± 0.18	3.85 ± 0.25	4.82 ± 1.02	5.50 ± 2.62
2	1.5	0.62 ± 0.44	0.30 ± 0.08	0.41 ± 0.25	0.24 ± 0.04	0.66 ± 0.47	0.80 ± 0.25	5.09 ± 0.39	2.44 ± 0.16	8.21 ± 13.31	8.13 ± 2.23
	3	0.47 ± 0.14	0.42 ± 0.02	0.25 ± 0.02	0.21 ± 0.01	0.53 ± 0.16	0.50 ± 0.13	4.93 ± 0.83	2.44 ± 0.64	10.49 ± 3.59	5.81 ± 1.55
3	0.5	0.10 ± 0.02	0.14 ± 0.01	0.10 ± 0.02	0.11 ± 0.01	1.00 ± 0.28	0.79 ± 0.09	0.28	0.39 ± 0.28	2.80 ± 0.56	2.79 ± 2.01
	1.5	0.21 ± 0.01	0.16 ± 0.02	0.16 ± 0.04	0.14 ± 0.07	0.76 ± 0.19	0.88 ± 0.45	2.68 ± 0.86	1.83 ± 0.90	12.76 ± 4.14	11.44 ± 5.81
	3	0.24 ± 0.02	0.43 ± 0.04	0.06 ± 0.04	0.20 ± 0.01	0.25 ± 0.17	0.47 ± 0.05	3.77 ± 0.23	3.53 ± 0.17	15.71 ± 1.65	8.21 ± 0.86
4	1.5	0.16 ± 0.03	0.18 ± 0.02	0.19 ± 0.05	0.16 ± 0	1.19 ± 0.38	0.89 ± 0.10	1.31 ± 0.48	0.79 ± 0.10	8.19 ± 3.37	4.39 ± 0.74
	3	0.17 ± 0.03	0.16 ± 0.02	0.20 ± 0.04	0.17 ± 0.03	1.18 ± 0.31	1.06 ± 0.23	2.60 ± 0.55	1.06 ± 0.30	15.29 ± 4.21	6.63 ± 2.05
5	1.5	0.16 ± 0.01	0.14 ± 0.01	0.16 ± 0.01	0.14 ± 0.01	1.00 ± 0.01	1.00 ± 0.10	1.47 ± 0.06	0.53 ± 0.05	9.19 ± 0.69	3.79 ± 0.45
	5	0.15 ± 0.01	0.14 ± 0.01	0.15 ± 0.01	0.12 ± 0.02	1.00 ± 0.01	0.86 ± 0.21	1.72 ± 0.08	1.63 ± 0.31	11.47 ± 0.93	11.64 ± 2.36

NOTE: Chlorophyll *a* and phaeophytin levels (mg/m^3) represent the means ($\pm SD$) of duplicate analyses from 2 days. Primary production rates (mg $C/m^3/hr$) represent the means of 2 light and 1 dark bottle on each of 2 days. Productivity index numbers (mg C/mg chlorophyll *a*/hr) were calculated using the means of the productivity and chlorophyll *a* values for each depth and tidal condition.

Model 1042 gas-flow Geiger–Müller counter. Zooplankton samples were collected by replicate horizontal tows with a 0.5-m-diameter, 212-μ-mesh net equipped with a flowmeter. Enteric bacterioplankton assessments (total and fecal coliforms and fecal streptococci) were made according to the procedures described by American Public Health Association (1975) and Millipore Corporation (1973). Surface and subsurface (3 m) samples were taken at 12 locations within the harbor. Confidence limits (Δz) for the productivity indices production/chlorophyll a and phaeopigment/chlorophyll a, given as the ratios of means, were calculated from the expression $\Delta z = z\sqrt{(\Delta x/x)^2 + (\Delta y/y)^2}$, where z is the mean ratio value and Δx and Δy are the confidence limits on the numerator of the ratio, x, and the denominator of the ratio y, respectively.

RESULTS

Generally, low phytoplankton biomass levels, ranging from 0.06–0.70 mg chlorophyll a/m^3, prevail within the harbor (Table 1). Biomass is lowest at the surface (0.5m) within the brackish water layer. Below this layer, chlorophyll a levels show slight but distinct increases and approach levels frequently encountered in Hawaiian neritic environments. Within the subsurface oceanic waters of the harbor, there is a general tendency for phytoplankton standing stocks to increase with greater distance from the ocean. At the innermost stations (1 and 2), biomass levels were about 2.5 times greater than those of the outer basin and displayed comparatively little vertical variation. In the deeper outer basin, which displays a less tidally variable thermohaline structure, the chlorophyll a maximum occurs within 2.5–4.5-m interval (Figure 1b). No systematic variation of chlorophyll levels is apparent among samples taken in the early morning (falling tide), noon (rising tide), or late afternoon, and levels within the harbor entrance channel were very similar to those of the adjacent coastal waters. Comparison of biomass levels reported in Table 1, taken

in February, with those from a reconnaissance the previous September (Oceanic Institute 1975a) shows no apparent seasonal differences in the phytoplankton stocks within the harbor. Phaeopigments, representing degradation products of chlorophyll, were generally higher in the inner provinces of the harbor, coinciding with increased chlorophyll a and zooplankton levels (Table 2), and greater thermohaline variability (Bienfang 1980). Phaeopigment/chlorophyll a ratios, however, were highest in the surface waters and increased in the seaward direction. Determination of phaeophytin/chlorophyll a ratios taken at 1-m intervals throughout the water column at sunrise and sunset showed high surface values in each case but no consistent trend with depth or time of day.

Phytoplankton productivity rates within the harbor are generally low, displaying small but distinct increases over rates in the adjacent coastal waters. Surface (0.5 m) production rates within the brackish water layer, averaging 0.40 mg $C/m^3/hr$, are below levels outside the harbor, and reflect both lower biomass and less favorable growth conditions (e.g., low temperature and salinity and high light intensity) characteristic of the harbor surface waters. Harbor production values in the subsurface waters range from 0.79 to 5.09 mg $C/m^3/hr$, compared with mean productivity rates of 1.34 mg $C/m^3/hr$ outside the harbor (Table 1). As observed in the phytoplankton standing stocks, production rates show a trend of increasing levels with increasing distance from the ocean. Averaged subsurface production rates in the back reaches of the harbor (stations 1 and 2) are about 1.5 times greater than those at the outer harbor stations (3 and 4). Comparison of morning versus afternoon productivity at both inner and outer harbor locations suggests 40 percent higher morning production rates. Averaged morning and afternoon subsurface values in the back basin area were 4.03 and 2.79 mg $C/m^3/hr$, respectively, and 2.59 and 1.80 mg $C/m^3/hr$, respectively, in the outer basin. Higher morning values coincide with conditions of falling tide, greatest vertical mixing, and highest incident radiation.

TABLE 2

COMPOSITION AND ABUNDANCE (MEAN ± SD) OF ZOOPLANKTON AT HONOKOHAU HARBOR, HAWAII

		HARBOR	
TAXONOMIC GROUP	COASTAL OCEAN	OUTER BASIN	INNER BASIN
Copepods	195.12 ± 2.95	496.72 ± 7.4	4,807.89 ± 404.11
Mysids	—	0.66 ± 0.03	2.65 ± 0.65
Euphausids	0.04 ± 0.04	0.02 ± 0.02	—
Shrimp zoea	0.08 ± 0.08	0.02 ± 0.02	—
Shrimp larvae	0.32 ± 0.14	0.46 ± 0.13	0.26 ± 0.26
Crab zoea	1.06 ± 0.16	1.50 ± 0.42	1.01 ± 0.01
Amphipods	0.03 ± 0.03	—	—
Chaetognaths	2.69 ± 0.68	0.04 ± 0.04	—
Polychaetes	—	0.02 ± 0.02	0.20 ± 0.20
Oikopleura sp.	0.23 ± 0.01	—	—
Doliolids	0.14 ± 0.02	—	—
Siphonophores	0.07 ± 0.01	—	—
Ctenophores	—	—	—
Ostracods	0.17 ± 0.05	0.02 ± 0.02	—
Bivalve larvae	0.78 ± 0.35	0.04 ± 0.04	392.88 ± 59.98
Gastropod larvae	2.00 ± 0.24	0.84 ± 0.21	518.05 ± 0.51
Fish eggs	3.28 ± 0.60	0.02 ± 0.02	—
Fish larvae	—	0.32 ± 0.10	1.39 ± 0.39
Total organisms/m³	206.09 ± 2.43	500.75 ± 7.76	5,744.31 ± 464.66
Dry weight (mg/m³)	5.62 ± 2.00	5.54 ± 1.03	32.63 ± 1.15

(Meteorological conditions common to this coastal region characteristically produce clear, sunny mornings and overcast afternoons which clear again in the early evening.) Productivity rates increase with increasing depth to 3.0 m in both morning and afternoon samples. The average harbor productivity rate at 1.5 m is 3.13 mg C/m³/hr in the morning and 1.85 mg C/m³/hr in the afternoon as compared with 3.0-m values of 3.49 and 2.72 mg C/m³/hr for morning and afternoon, respectively. A supplemental vertical profiling of nutrients, phytoplankton biomass, productivity, and productivity index taken at 1.0-m intervals throughout the 5.5-m water column of the outer basin (station 3) describes a more detailed picture of the harbor phytoplankton activity (Figure 1). Production rates increase with increasing depth to 3.5 m, where maximum photosynthesis occurs and below which rates decline; biomass levels, on the other hand, remain higher and fairly constant throughout the 2.5–4.5-m range. It is interesting to note that production rates at 1.5 and 5.5 m (Figure 1) within the harbor are similar to values attained at these depths outside the harbor (Table 1).

The productivity indices (PI), also called assimilation numbers, range from 2.8 to 15.71 mg C/mg chlorophyll *a*/hr throughout the harbor (Table 1). The PI values are lowest in the surface, brackish layer, reflecting the low production rates found there. Harbor PI values show a general tendency to increase with increasing depth and with proximity to the ocean. Following the trend of productivity rates, PI values are also highest in the morning samples. The supplemental profile at station 3 (Figure 1) suggests a PI maximum at 3.5 m, and comparison of values at 1.5 and 5.0 m with those at station 5 (Table 1) imply that comparable conditions for photosynthesis prevail at the two locations. The PI values are generally lower in the back regions of the harbor, where productivity rates and standing stocks were highest.

Zooplankton biomass in Honokohau Harbor was estimated from dry weight measurements by enumeration of individual representative taxonomic groups (Table 2). The
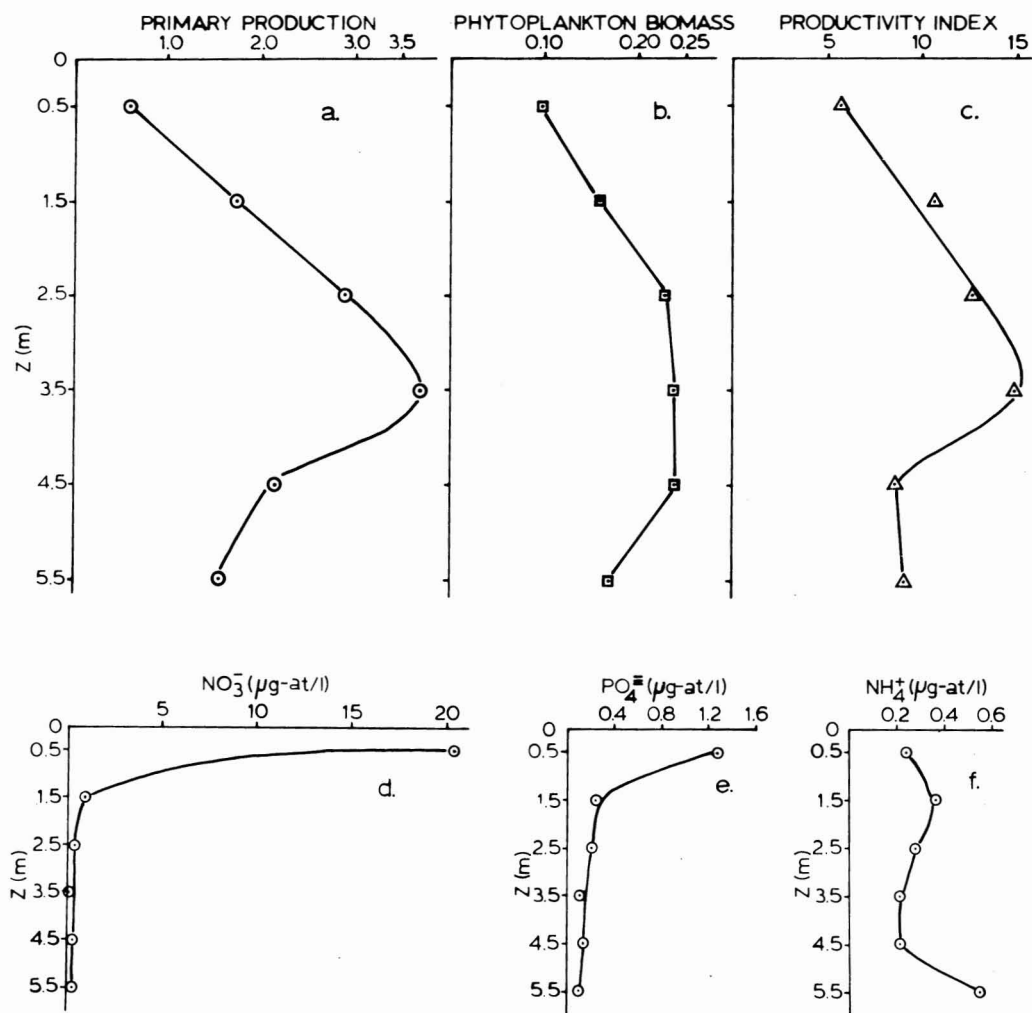
FIGURE 1. Vertical profiles of phytoplankton and nutrient parameters in the outer basin of Honokohau Harbor. Primary production, phytoplankton biomass, and productivity index values are in units of mg $C/m^3/hr$, mg chlorophyll a/m^3, and mg C/mg chlorophyll a/hr, respectively.

results of both measurements show an increase of biomass in the inner berthing basin as compared to the outer basin and adjacent coastal waters. Mean zooplankton dry weight is 5.8 times greater for the inner basin than for the oceanic station, and this figure is in good agreement with the increase of phytoplankton biomass at this location. Carnivorous organisms are found to be less abundant in the inner basin than in the outer basin or coastal waters, and high zooplankton densities there may also be due to the

reduced grazing pressure. Chaetognaths were collected at the two outer tow stations, while none were found in the inner basin; the fish population was also smaller both in numbers and size of individuals there than at outer stations (Oceanic Institute 1975a).

A general trend of increasing zooplankton density and decreasing taxonomic diversity occurs from the coastal station to the inner basin. Total numbers of organisms increase by a factor of 28, due mostly to the dominance of a small copepod species, *Acartia*

sp., in the inner basin. Many zooplankton species have a low tolerance to the reduced salinities that are likely to be encountered in the inner basin, while *Acartia* sp. is reportedly found in waters of varying salinities and appears to be well adapted to this estuarine environment. The shelled larvae of bivalves and gastropods are found in high numbers only in the inner basin, and this may be due to the relatively shallow water and increased mixing.

Enteric bacterioplankton levels (total coliforms, TC; fecal coliforms, FC; and fecal streptococci, FS) were measured in both the surface and subsurface waters throughout the harbor on four separate occasions. Enteric bacterioplankton are an index fecal contamination that may be transmitted to waters by storm run-off, raw sewage discharge, or inadequate sewage treatment. At the time of these surveys, 51 boats, including no live-aboards, were moored within the harbor and there was a comfort station located on the peninsula separating the two berthing basins. The TC levels within the harbor were generally low (always < 500 TC/100 ml) and easily within limits established for class A waters (< 1000 TC/100 ml); the majority of the samplings were below class AA limits (< 70 TC/100 ml). The TC levels were generally higher in the surface waters, possibly indicating slower die-off rates due to lower salinity, proximity to bacterial inputs, and/or retention within the strongly defined surface layer. The FC levels were much lower than TC levels in all surveys and ranged from 0 to 165 FC/100 ml (the high end of this range was represented by a single sample). Mean FC levels within the harbor were about 5 FC/100 ml and easily conform to class A standards (< 200 FC/100 ml). The FS levels were also low (about 4 FS/100 ml). These measurements were taken to gain information regarding the probable nature of the enteric bacterial origin. The ratio of fecal coliform to fecal streptococci (FC/FS) is a means of identifying the probable origin (e.g., human versus nonhuman) of the measured enteric bacteria; waters that show FC/FS > 1 are more likely to contain wastes of human origin and the likelihood increases as the FC/FS ratio increases. The majority of the FC/FS ratios show that enteric bacterial levels within the harbor are attributable to nonhuman sources.

However, there were several instances in which predominantly human and/or mixed fecal contamination were evident. Details of the bacteria data can be found in Oceanic Institute (1975b). These data indicate that leaching is occurring from the existing septic tank/cesspool facility on the peninsula separating the two berthing basins. The extremely high gross permeability of lavas in such environments permits free water movement into and out of the harbor walls transporting relatively fresh sewage effluents to the harbor waters. The peninsular location amplifies this hazard by providing near maximum surface area for such transport. Data suggest that the co-occurrence of a small harbor patron population and rapid flushing of this small basin prevent the fecal pollution problems from being acute in the face of this fecal input mechanism.

DISCUSSION

Honokohau Harbor shows remarkably oligotrophic planktonic characteristics considering the eutrophying potential represented by groundwater nitrate and phosphate inputs. These observed pristine conditions are maintained within the shallow embayment by the rapid harbor flushing rates promoted by the persistent outflow of the surface layer (Gallagher 1980), a strongly stratified surface nutricline (Bienfang 1980), and the grazing activities of higher trophic levels inhabiting the harbor (E. A. Kay, personal communication, 1978, Brock 1980). The absence of sediment-laden surface run-off and/or stream input promotes water clarity and the generally low enteric bacterioplankton levels. The paucity of non-biological particulate matter, which would affect herbivorous grazing rates and efficiencies, may also promote the healthy zooplankton populations within the harbor. Turbidity is positively correlated with chlorophyll *a* levels ($p = 0.01$), and phyto-

plankton biomass is primarily related to turbidity variations within this embayment.

Phytoplankton biomass and productivity are not of the potential magnitude suggested by the proximate nitrate and phosphate concentrations, because most of these nutrients pass directly out of the harbor in the surface outflow. Phytoplankton characteristics do, however, show relationship to the peculiar thermohaline and nutrient stratification. Harbor configuration and location of greatest groundwater influx at the innermost reaches of the basin maintain a rapid, continual outflow of the nutrient-rich surface water and reduce the degree of assimilation by the resident phytoplankton community. This persistent outflow also entrains oceanic water from below which, together with turbulent mixing, account for the phaeophytin and chlorophyll in the surface layer.

Surface phaeophytin/chlorophyll *a* ratios in the major basins show consistently high values. This is anomalous because phaeophytin is rapidly degraded to unmeasurable byproducts when exposed to sunlight. Thus, the continual presence of high ratios must result from a persistent process, for although chlorophyll levels are low, the concurrent phaeophytin reduction by light would tend to make phaeophytin levels correspondingly lower. Since zooplankton populations were most abundant in the subsurface waters (Oceanic Institute 1975a), there is an implication that phaeophytin production arises from nongrazing causes. A plausible explanation is the lysing of marine phytoplankton cells due to osmotic imbalance during entrainment into the lower saline surface layer. Ratios at the most oceanic stations (4 and 5) were approximately equal to 1, regardless of the time of day; while subsurface values in the two berthing basins were considerably lower, indicating that the higher chlorophyll levels at these locations were more of a determinant on phaeophytin/chlorophyll *a* ratios than the increased grazing pressure exerted by the considerably higher zooplankton stocks at these areas (Table 2). This suggests that phenomena (e.g., hydrological) affecting phytoplankton biomass and growth rates are exerting stronger control over the phytoplankton activity than grazing activities of the herbivorous zooplankton. We also observed a decline in water clarity throughout the day; yet vertical profiling at sunrise and sunset showed similar ratios throughout the water column. Because phaeophytin results from the zooplankton grazing of chlorophyll-containing cells, one would expect higher sunrise ratios due to both removal of chlorophyll and production of phaeophytin through the evening. We suggest that advective processes are having a pronounced effect on the phytoplankton standing stocks by the continued transport of phytoplankton from the harbor. The interpretation is that through the evening, when production is nil, harbor flushing and entrainment of chlorophyll and phaeophytin from the subsurface waters in the continual surface outflow are largely responsible for the higher morning transparency. This physical removal of both chlorophyll and phaeophytin may account in part for the lack of sunrise–sunset phaeophytin/chlorophyll *a* variations in the face of obvious chlorophyll-related turbidity differences.

Despite high nitrogen and phosphorus levels in the surface waters, it appears that nutrient availability is likely to be a controlling parameter on the subsurface phytoplankton populations. The vertical transport of nutrients downward is restricted by the density stratification between the nutrient-rich surface and the nutrient-poor oceanic waters, and by the gradual upward entrainment of subsurface waters in the outflowing brackish layer. Nutrient control of harbor phytoplankton activity is supported by the intermediate depth productivity and PI maxima (Figure 1) and the high production rates in the back basin (Table 1) where more complete vertical mixing results in reduced stratification and higher subsurface nutrient levels (Bienfang 1980). Throughout most of the harbor, nutrients are transported downward by molecular diffusion and/or turbulent mixing; the degree of diffusion and/or mixing varies inversely with increasing vertical distance from the interface. Strong incident sunlight also affects production profiles through surface photoinhibition,

but considering the shallow water column (5.5 m) and the generally high water transparency, it seems unlikely that inadequate sunlight could limit production rates in the 3.5–5.5-m region (Figure 1). We believe the intermediate depth maximum of phytoplankton activity results from the co-occurrence of increased nutrient availability to a region receiving suitable (noninhibiting, nonlimiting) solar radiation. The enhanced nutrient input to this region need not necessarily be reflected in ambient nutrient levels (which were lowest at 3.5 m) if phytoplankton assimilation rates are of the same order as the delivery rates. Also, nutrient profiling on other occasions (Bienfang 1980) than that reported in Figure 1 showed considerably higher ambient nutrients (about 1 μg-at NO_3^-/liter and 0.30 μg-at PO_4^{3-}/liter) at 3.0 m at this location, indicating that the low nutrients depicted in Figure 1 may not be a persistent feature. High primary productivity rates in the inner harbor regions, which display greatest mixing and weakest stratification, may reflect higher nutrient inputs to the subsurface populations. This supports the belief that nutrient availability may be controlling production in the subsurface waters of the harbor in general. It is not known to what extent low and tidally variable temperature and salinity levels in this region affect the resident phytoplankton growth rates. Nonlimiting subsurface nutrients in the back regions imply alleviation of nutrient control there and suggest the increased effects of grazing and flushing in controlling phytoplankton stocks. The response of the second trophic level, which shows increases in biomass in regions of higher primary standing stocks, suggests a healthy environment in which growth-affecting parameters other than food availability (e.g., oxygen, heavy metals) are suitable to permit natural population-dynamic responses.

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