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Light driven seasonal patterns of chlorophyll and nitrate in the lower euphotic zone of the North Pacific Subtropical Gyre

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Abstract

The euphotic zone below the deep chlorophyll maximum layer (DCML) at Station ALOHA (a long-term oligotrophic habitat assessment; 22°45′N, 158°00′W) transects the nearly permanently stratified upper thermocline. Hence, seasonal changes in solar radiation control the balance between photosynthesis and respiration in this light-limited region. Combining profiles of radiance reflectance, algal pigments, and inorganic nutrients collected between January 1998 and December 2000, we explore the relationships between photosynthetically available radiation (PAR), phytoplankton biomass (chlorophyll *a*), and the position of the upper nitracline in the lower euphotic zone. Seasonal variations in the water-column PAR attenuation coefficient displace the 1% sea-surface PAR depth from approximately 105 m in winter to 121 m in summer. However, the seasonal depth displacement of isolumes (constant daily integrated photon flux strata) increases to 31 m due to the added effect of changes in sea-surface PAR. This variation induces a significant deepening of the DCML during summertime with a concomitant increase in chlorophyll *a* and the removal of 36 mmol m^{-2} inorganic nitrogen [NO_3^- + NO_2^-] in the 90–200-m depth range, equivalent to approximately 34% of the annual flux of particulate nitrogen collected in sediment traps placed at 150 m. We conclude that in this oceanic region the annual light cycle at the base of the euphotic zone induces an increase in the phototrophic biomass analogous to a spring bloom event.

Based on the effects of light, the water-column has been historically divided into three major zones: (1) a euphotic zone where light intensity is sufficient to support net photosynthesis, (2) a disphotic or twilight zone where light intensity cannot support net photosynthesis but is sufficient to stimulate visual organs allowing the perception of forms, and (3) an aphotic zone where light is, for all practical purposes, absent. In 1956 John Ryther defined the depth of the euphotic zone as the depth at which the photon flux equals 1% of the flux measured just above the air–sea interface. In a footnote following the definition he warned ''Thus the euphotic zone, as used here, has no biological significance other than defining the water mass below which no appreciable photosynthesis can occur'' (Ryther 1956). Since the publication of Ryther's definition, the euphotic zone depth has been routinely characterized in terms of sea-surface irradiance percentage levels (Parsons et al. 1984; Walsh et al. 1995; Smith and Kemp 2001).

The reason for Ryther's warning arises from the temporal variability in solar irradiance and the linear dependency of photosynthesis on photon flux under light-limiting conditions. The percentage light level depth is mainly dependent on the water-column light attenuation and provides information regarding the relative depth distribution of light, not the absolute photon flux. Hence, any given light level depth expressed as a constant percentage of sea-surface photosynthetically available radiation (PAR) may experience signifi-

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cant variance in daily integrated photon fluxes and photosynthetic rates due to changes in solar irradiance resulting from the solar seasonal cycle and cloud coverage variability (Banse 1987).

Two other important terms used to characterize water-column community properties are the compensation and critical depths. Both of these concepts are based on biological energy balances. While the compensation depth is defined as the depth where the photosynthetic rate equals the photoautotrophic respiration for obligated photoautotrophs, the critical depth is equivalent to the depth where integrated water-column photosynthesis equals integrated water-column respiration (Sverdrup 1953; Smetacek and Pasow 1990; Platt et al. 1991; Siegel et al. 2002). Both these concepts are physiologically and ecologically sound. However, neither is easily measured in the field. By comparison, the percentage light level depth is relatively easy to measure but difficult to interpret from a biological perspective. Nevertheless, Parsons et al. (1984) observed that the light level at the compensation depth was usually two orders of magnitude lower than the sea-surface irradiance and concluded that its depth could be approximated by the 1% light level depth.

In oceanic regions where the base of the euphotic zone remains stratified, day to day and seasonal variations in the photon flux can have significant effects on the balance between photosynthesis and respiration in the light-limited region of the euphotic zone. In these regions, the position of the top of the nitracline must be controlled by the balance between biological nutrient uptake resulting from photosynthesis, in situ nutrient regeneration due to microbial remineralization, and the diffusion of allochthonous nutrients from depth. Hence, if the depth of constant light intensity (isolume) changes significantly with seasons as a result of changes in solar irradiance or water-column light attenuation, we should expect a dynamic interaction between the vertical displacement of isolumes and the position of the nitracline.

In these oceanic regions, new production (sensu Dugdale and Goering 1967) represents a small fraction of the total integrated primary production, generally less than 10% (Vezina and Platt 1987; Letelier et al. 1996). Also, the observed chemical gradients indicate that the upward diffusive flux of nutrients is used by photoautotrophs at or below the 1% light level depth. This observation suggests that most, if not all, new production supported by the diffusion of nutrients takes place in the lower euphotic zone (Lewis et al. 1986; Goldman 1993). Hence, even if the contribution by the phytoplankton assemblage in the lower euphotic zone to the water-column integrated primary production is negligible, as stated by John Ryther in 1956 and confirmed by numerous field studies since, it may still represent a significant fraction of the new production. Under a permanently stratified lower euphotic zone scenario, seasonal differences in the position of the nitracline driven by changes in the depth position of isolumes could be used to estimate a minimum contribution of this lower euphotic zone community to new production.

One oceanic region where the depth of the mixed layer rarely penetrates the base of the euphotic zone is the North Pacific subtropical gyre (NPSG; Winn et al. 1995). Since October 1988, the Hawaii ocean time-series (HOT) program has conducted an extensive series of monitoring cruises at nearly monthly intervals to Station ALOHA (a long-term oligotrophic habitat assessment, 22°45′N, 158°00′W; Karl et al. 2001; Fig. 1). The stated goal of this time-series effort is to identify and characterize the processes that drive the biogeochemical cycles in the NPSG (Karl 1999).

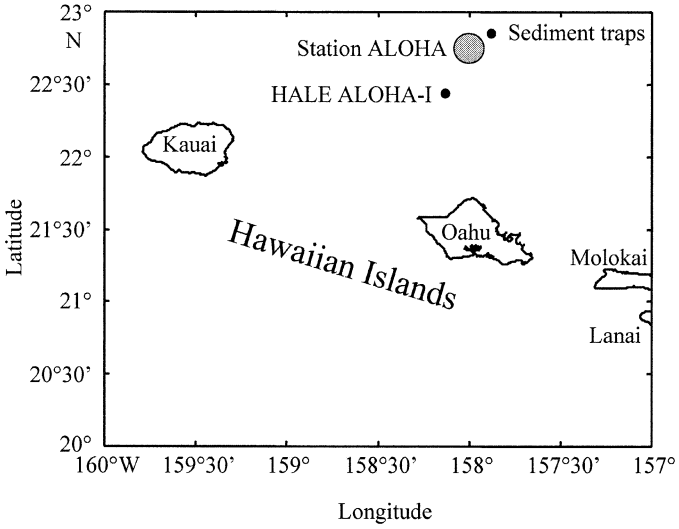


Fig. 1. Geographical location of Station ALOHA also showing the location of the ALOHA-moored sediment traps and the position of a physical and biochemical mooring (HALE ALOHA) deployed between 1997 and 1999.

Since February 1998 a profiling reflectance radiometer (PRR, Biospherical Instruments) has been deployed monthly during HOT cruises in order to characterize the variability in water-column light penetration during these cruises (Nahorniak et al. 2001). In the present study we describe and analyze a subset of the PRR results in the context of the physical and biogeochemical HOT data set. Our aim in the present paper is to describe and discuss how seasonal variability in solar irradiance and changes in water-column transparency may affect the flow of nutrients and energy into the lower euphotic zone.

Methods

Radiance reflectance profiles were obtained using a PRR-600 profiling unit and a PRR-610 surface reference radiometer (Biospherical Instruments). The PRR-600 simultaneously measures downwelling irradiance and upwelling radiance with 10-nm bandpass filters centered at 412, 443, 490, 510, 555, and 665 nm as a function of pressure, where pressure is used as a proxy for depth. It also measures in situ temperature and PAR and includes an upwelling radiance sensor with a 10-nm bandpass filter centered at 683 nm to monitor the solar-induced chlorophyll fluorescence. Sea-surface PAR and downwelling irradiances were obtained concurrently with a PRR-610 instrument and were used to normalize downwelling profiled measurements.

PRR casts were performed in order to coincide with the time of overpasses of the ocean color satellite sensor *SeaWiFS*, between 1200 and 1400 h, Hawaii Standard Time. The profiler was deployed as far as possible from the ship

structure using the extended boom on the ship's crane to avoid ship's shadow. Once properly positioned at the sea surface, the instrument package was lowered by hand to depths between 120 and 170 m. At the beginning of each new deployment, the profiling unit was allowed to acclimatize to the sea-surface temperature for approximately 2 min before the beginning of the profile. Dark measurements were collected to correct for dark current background. The PRR-610 deck reference unit was also positioned to minimize ship structure shadows. The PRR sensors were calibrated by Biospherical Instruments approximately every 6 months.

Data corresponding to values collected when the profiling unit had tilt or roll angles greater than 5° or for depths shallower than 5 m were removed from each profile. The 1% light level depth for PAR was calculated as the depth where the PRR-600 PAR measurement corresponds to 1% of the PAR value recorded by the PRR-610 deck unit. We used this depth value to further calculate a mean light attenuation (K_{PAR}) for the upper euphotic zone. Continuous profiles of chlorophyll *a* concentrations (Chl *a*) and attenuation at 440 nm due to colored dissolved organic matter (CDOM) were derived from these PRR profiles according to Nahorniak et al. (2001).

The mooring record reported here is a subset of the HALE ALOHA (Hawaii Air-sea Logging Experiment, A Long-term Oligotrophic Habitat Assessment) mooring effort that took place between 1997 and 2000. The description of this mooring effort and its configuration can be found in Letelier et al. (2000). A climatological sea-surface solar irradiance cycle was derived from continuous solar irradiance measurements at the mooring obtained between January 1997 and May 1998 and the derivation of the theoretical solar elevation and daylength cycles at 22°45′N (Kirk 1994). The theoretical solar elevation and daylength cycles are not significantly different between Station ALOHA (22°45′N) and the HALE ALOHA mooring position (22°25′N). The mooring solar irradiance was divided in 7-d bins from which the mean and standard deviation daily integrated irradiance was calculated. A 7-d running average of the theoretical annual daily solar irradiance cycle was then compared and adjusted to the mooring data based on the maximum and minimum values derived from the 7-d bin record (Fig. 2). The resultant irradiance cycle did not differ from a daily cycle of solar radiation calculated from the classical astronomical formula (Brock 1981) employing the correction of the solar constant by Duffie and Beckman (1980).

In order to remove the high frequency variability due to clouds that affects the depth profiles of absolute photon flux measured during a particular cast, profiles of PAR were calculated using the climatological solar irradiance cycle and the relative propagation of PAR with depth derived from the PRR profiles:

$$PAR_z = PAR_0 \times PAR(PRR)_z \times (PAR[PRR]_0)^{-1}$$

where PAR_z is the photosynthetically available radiation calculated for depth z, PAR_0 is the theoretical sea-surface PAR derived from the climatological sea-surface solar irradiance seasonal cycle, and $PAR(PRR)_z$ and $PAR(PRR)_0$ are the instantaneous downwelling irradiances recorded by the profiling and deck reference units, respectively.

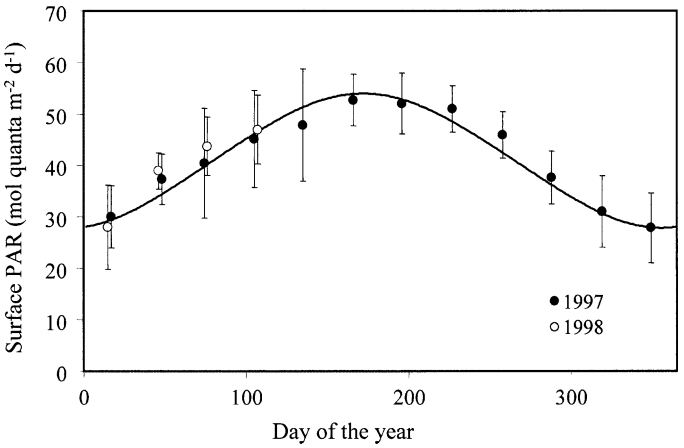


Fig. 2. Seasonal variability of daily integrated sea-surface photosynthetically available radiation (PAR) at Station ALOHA. Circles and error bars correspond to monthly means and standard deviation. Solid line represents a 7-d running average of the climatological PAR model (*see text for details*).

Physical and chemical characterizations of the water column were derived from the approximately monthly HOT program core measurements performed at Station ALOHA (Karl and Lukas 1996). In our present study the effect of tidal and near-inertial period oscillations in single profiles has been minimized by extrapolating the depth at which particular samples are collected to an average 0–1,000-m density profile derived from a repeated series of 12 to 18 hydrocasts collected at approximately 3-h intervals (Dore and Karl 1996; Letelier et al. 2000). During each cruise, these repeated casts cover three semidiurnal tidal and a complete inertial period (f^{-1} = 31.03 h at Station ALOHA).

A Sea-Bird 911-plus conductivity–temperature–depth (CTD) probe, equipped with several external and internal sensors and mounted in an aluminum frame containing 24 polyvinyl chloride sample bottles, was used during each cruise to obtain high-resolution temperature, conductivity, fluorescence, and dissolved oxygen depth profiles. Discrete samples were collected for the biological and chemical characterization of the water column, as well as for sensor calibration purposes.

Discrete samples were collected for the determination of Chl *a* concentration by the fluorometric procedure (Strickland and Parsons 1972) as described by Letelier et al. (1996). These fluorometric determinations were used to calibrate the continuous chlorophyll fluorescence profiles in order to obtain a high-resolution characterization of the DCML. Dissolved inorganic nitrogen concentrations were determined on a four-channel autoanalyzer [NO_3^- + NO_2^-] for samples collected below 100 m. The low concentrations observed at shallower depth required the use of the highly sensitive chemiluminiscent method (Garside 1982) as modified by Dore and Karl (1996). Because of the vertical displacement of isopycnals within a given cruise (Letelier et al. 1993; Karl and Lukas 1996; Dore and Karl 1996) the depths of discrete samples collected in any particular hydrocast were corrected

to the average 0–1,000-m density profile, as described above. One consequence of this process is that the resulting profiles do not have standard depths.

During each cruise the depth of the DCML at Station ALOHA was determined as the depth of maximum fluorescence below 60 m, derived from the mean continuous profile of chlorophyll fluorescence corrected for short-term isopycnal displacements. To calculate the position of the top of the nitracline, we generated a 5-m depth interval trace by cubic spline interpolation (Press et al. 1992) through the combined depth corrected $[NO_3^- + NO_2^-]$ profiles collected during each cruise. The top of the nitracline was determined from this cubic spline interpolation and defined as the shallowest depth at which the $[NO_3^- + NO_2^-]$ depth gradient exceeds 2 nmol kg^{-1} m^{-1}. The mixed layer was defined based on the average density profile for each cruise as the depth range where the density gradient is less than 0.005 kg m^{-4} (Letelier et al. 1996).

In order to contrast winter versus summer conditions, data collected during periods of the year when climatological sea-surface PAR is lower than 32 mol quanta m^{-2} d^{-1} (winter) and greater than 47 mol quanta m^{-2} d^{-1} (summer) were selected (Table 1). In addition, summer month cruises when subsurface blooms were observed (HOT-96 and HOT-116) were considered as special summer conditions because of the significant shading effect that these blooms produce.

Results

During the present study, both temperature and density at Station ALOHA display significant seasonal trends in the upper 100 m of the water column (Fig. 3A,B). The average temperature in the mixed layer varies between 23.1°C (SD = 0.33°C, $n = 5$) in January–February and 25.3°C (SD = 0.6°C, $n = 6$) in July–August. The mean mixed-layer depths observed during these annual extremes are 86 m (SD = 15.8 m, $n = 5$) and 44 m (SD = 8.8 m, $n = 6$), respectively. Although the seasonal temperature signal is strong in the upper euphotic zone (>2°C), it is not discernible below the 100-m isobath (Fig. 3B).

Sea-surface mean monthly solar irradiance derived from mooring measurements also displays a strong seasonal pattern with extremes of 27.8 and 52.8 mol quanta m^{-2} d^{-1} measured during December and June, respectively (Fig. 2). This seasonal cycle is also observed in the distribution of light within the euphotic zone (Fig. 3C). Isolume depths, defined here as line depths of constant daily integrated photon flux, have a seasonal depth variation of approximately 30 m.

Superposed on the seasonal cycle in the depth position of isolumes we observed a shoaling during the summer of 1998 and 2000 (Fig. 3C). In both occasions the summer deviations are recorded during cruises when subsurface phytoplankton blooms are detected close to the base of the mixed layer (Fig. 4). With the exception of these summer bloom events, the annual average of daily photon flux measured at the 1% light level (0.415 mol quanta m^{-2} d^{-1}) is located at approximately 120-m depth during summer (when surface PAR > 47 mol quanta m^{-2} d^{-1}) and 90-m depth during winter (when surface PAR < 32 mol quanta m^{-2} d^{-1}; Fig. 5). Results from a model II linear regression indicate that, under nonbloom conditions, there is a significant relationship between the depth of this isolume and sea-surface PAR ($r^2 = 0.78$).

However, even though the seasonal depth position of a given isolume can be predicted from sea-surface PAR, changes in PAR alone are not sufficient to explain the magnitude of the observed isolume depth displacement. Variations in light attenuation coefficient (K_{PAR}) observed in the upper euphotic zone also contribute significantly to the observed seasonal cycle of light in the lower euphotic zone (Fig. 5). Previous HOT data analyses (Letelier et al. 1996, 2000) have assumed a constant K_{PAR} of 0.040 m^{-1} at Station ALOHA. If this assumption is correct, then the depth of the 0.415 mol quanta m^{-2} d^{-1} isolume should vary between 116 m in summer and 100 m in winter (surface PAR ≈ 52.8 and 27.8 mol quanta m^{-2} d^{-1}, respectively). Our present results suggest that, under nonbloom conditions, the mean euphotic zone K_{PAR} values are significantly greater in winter than in summer months ($K_{PAR} \approx 0.044$ and 0.037 m^{-1}, respectively; Fig. 5).

Both the position of the DCML, as detected from continuous chlorophyll fluorescence trace measurements, and that of the nitracline at the base of the euphotic zone display a significant displacement with the time of year (Fig. 6). While the mean position of the DCML during summer months under nonbloom conditions is located at 125 m (SD = 9 m), winter positions are found in the vicinity of 107 m (SD = 7 m; Table 1). Under bloom conditions the DCML broadens and its mean position shoals to 110 m. The top of the nitracline shoals from approximately 117 m (SD = 5 m) in summer to 91 m (SD = 15 m) in winter.

Discussion

Observations at Station ALOHA between 1998 and 2001 are consistent with a light driven seasonal cycle in phytoplankton biomass and nutrient dynamics in the lower euphotic zone. Furthermore, our results suggest that this dynamic is enhanced by an increase of the light attenuation in the upper euphotic zone during wintertime as a direct result of increased chlorophyll within the mixed layer. The rise in chlorophyll concentration in the upper euphotic zone has been attributed to phytoplankton photoadaptation in the mixed layer (Winn et al. 1995). Compared to the summer average irradiance in the mixed layer, the winter deepening of this layer combined with the seasonal reduction in sea-surface PAR decreases the mean light that is available for phytoplankton cells by a factor of 3 (Karl et al. 2002).

The additive effects of seasonal changes in sea-surface solar irradiance and water-column light attenuation at Station ALOHA result in a seasonal vertical displacement of isolumes of approximately 30 m (Figs. 3C, 5). However, this result is based on the assumption that K_{PAR} can vary between cruises but remains constant between the sea surface and the depth of the 1% light level during any given cruise. An alternative approach that takes into account changes in K_{PAR} due to the variability in chlorophyll concentration with depth uses attenuation coefficients for water and pigments (K_w and

Table 1. Climatological surface PAR, chlorophyll *a* concentration at the DCML, and mean depth position of the DCML and top of the nutricline during winter and summer HOT cruises conducted between 1 Jan 1998 and 31 Dec 2000 (Avg = average and SD = standard deviation). Summer bloom values in parentheses correspond to the DCML observed at the base of the mixed layer.

HOT cruise no.	Date	Climatological surface PAR (mol quanta m^{-2} d^{-1})	DCML [Chl *a*] (mg m^{-3})	DCML depth (m)	Top of nitracline (m)
Winter					
99	1 Nov 1998	31.9	0.56	100	103
100	8 Dec 1998	28.5	0.50	114	93
101	2 Jan 1999	27.7	0.38	116	90
110	14 Dec 1999	27.9	0.72	102	75
120	29 Nov 2000	29.5	0.66	104	73
212	20 Dec 2000	27.4	0.63	108	110
Average		28.8	0.58	107	91
SD		1.7	0.12	7	15
Summer nonbloom					
93	12 May 1998	47.5	0.68	136	115
94	17 Jun 1998	52.7	0.70	130	120
95	15 Jul 1998	52.1	0.68	128	110
105	9 May 1999	47.3	0.95	118	110
106	13 Jul 1999	52.1	0.90	128	117
107	13 Aug 1999	51.1	1.08	108	112
115	23 May 2000	49.2	0.71	136	120
117	25 Jul 2000	51.7	0.62	126	123
118	22 Aug 2000	49.7	0.66	116	123
Average		50.4	0.78	125	117
SD		2.0	0.16	9	5
Summer bloom					
96	9 Aug 1998	51.2	(0.51) 0.66	(42) 106	90
116	22 Jun 2000	52.6	(0.78) 0.67	(38) 112	88

K_c, respectively) derived from Morel (1988). When comparing these two methods, the maximum difference in depth for the isolume corresponding to 0.415 mol quanta m^{-2} d^{-1} is 1.3 m (data not presented).

Although a seasonal vertical displacement of 30 m represents a significant deepening of the euphotic zone, as defined by the 1% of surface irradiance criterion, short-term displacements of isopycnals due to tidal and near-inertial oscillations exceed this seasonal depth range at Station ALOHA. In consequence, phytoplankton assemblages in the lower euphotic zone may experience day to day variations in solar irradiance reaching eightfold as a result of these short-term vertical displacements (Karl et al. 2002). This variability could have significant effects on the nutrient fields. Nevertheless, there is a consistently tight coupling between the position of the DCML, as defined from the fluorescence trace, and a given isopycnal within the burst sampling period of HOT cruises (Letelier et al. 1993). Furthermore, nitrate profiles collected within a single cruise do not display significant differences when plotted as a function of density. The observed tight coupling with isopycnals for both the DCML and the upper nitricline within a given cruise suggests that the scale of response of the phytoplankton assemblage and its effect on the nutrient fields is significantly longer than an inertial period. For this reason we have not included the effects of these short-term isopycnal variations in the analyses of the seasonal light, nitrate, and chlorophyll fields.

The observed seasonal vertical displacement of isolumes is consistent with the observed position of the DCML and the upper nitracline during winter and summer. When chlorophyll and nitrate concentrations are plotted versus PAR (Fig. 7), the depth difference observed between winter and summer conditions (Fig. 6) disappears. In both seasons, the DCML is found at approximately 0.5 mol quanta m^{-2} d^{-1} and the top of the nitracline at 0.7 mol quanta m^{-2} d^{-1}. However, when comparing these light-normalized depth profiles, two significant differences remain: the magnitude of the DCML and the shape of the nitracline.

Differing from the mechanism that explains the summer decrease in chlorophyll in the upper euphotic zone, the enhanced DCML observed during this season is consistent with an increase in phytoplankton biomass (Letelier et al. 1993; Winn et al. 1995). Changes in chlorophyll concentration at a given isolume under stratified conditions are difficult to explain in terms of photoadaptation, unless one invokes an increase in the amplitude or frequency of isopycnal vertical displacements (Karl et al. 2002) or a change in community structure. Furthermore, the observed summer depletion in nitrate between 90 and 200 m supports a biomass-production increase hypothesis.

The increase in the DCML biomass from 0.58 mg Chl *a* m^{-3} (SD = 0.12 mg m^{-3}, $n = 6$) in winter to 0.78 mg Chl *a* m^{-3} (SD = 0.16 mg m^{-3}, $n = 9$; Table 1) in summer is statistically significant ($p < 0.05$). It suggests that the nitrate-based production in the 90–200-m depth range at Sta-

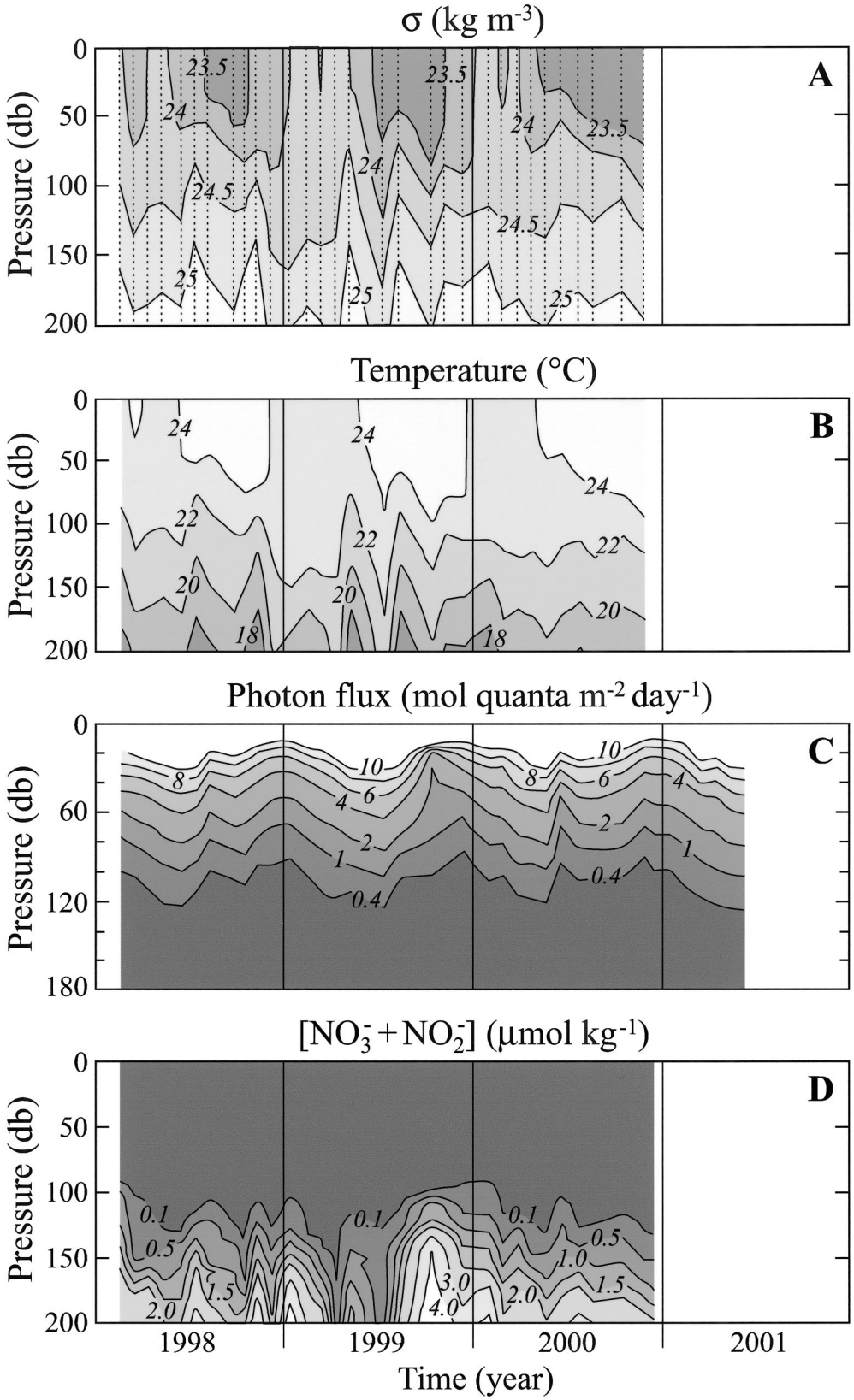


Fig. 3. Temporal evolution of the vertical distribution of (A) water density anomaly, (B) temperature, (C) photon flux, and (D) $[NO_3^- + NO_2^-]$. Vertical lines indicate 31 December.

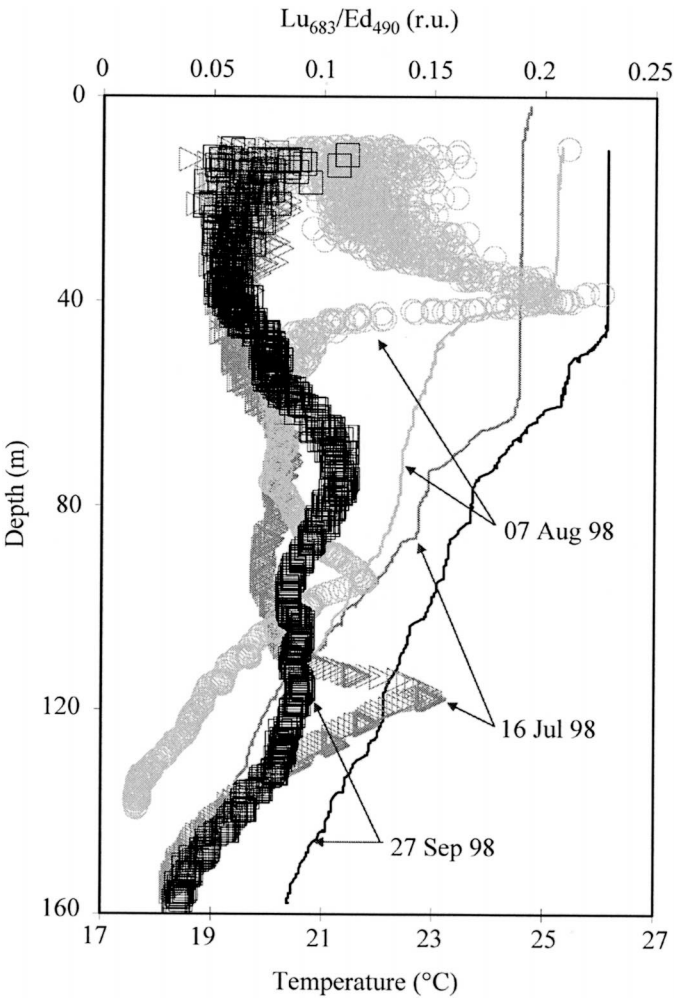


Fig. 4. Fluorescence signature of a summer subsurface bloom (August 1998) compared to profiles collected during July (squares) and September 1998 (triangles). The profiles represent natural fluorescence per unit available light (symbols) and temperature (lines). Note that the maximum fluorescence during August is positioned at 40 m, near the base of the mixed layer.

tion ALOHA has a seasonally driven component. This hypothesized seasonality is also consistent with the observed temporal erosion of the upper nitracline. The depth integration of the difference between the winter and summer Chl *a* below 90 m amounts to approximately 16.3 mg m^{-2} (Fig. 8A), or 42% of the mean integrated Chl *a* measured in the 90–200-m depth range during winter. Assuming C : Chl *a* and C : N ratios of 25 : 1 (w : w) and 6.6 : 1 (mol : mol), respectively (Christian et al. 1994; Hebel and Karl 2001), this net summer increase in Chl *a* requires 5.2 mmol N m^{-2}. The concomitant decrease in integrated $[NO_3^- + NO_2^-]$ (Fig. 8B) amounts to approximately 36 mmol N m^{-2}. Because this latter figure does not include new nitrogen available through diffusion or cross-isopycnal mixing at the base of the euphotic zone, it may be considered a lower limit estimate of the autotrophic production supported by allochthonous nitrogen.

The increase in chlorophyll below 90 m represents less

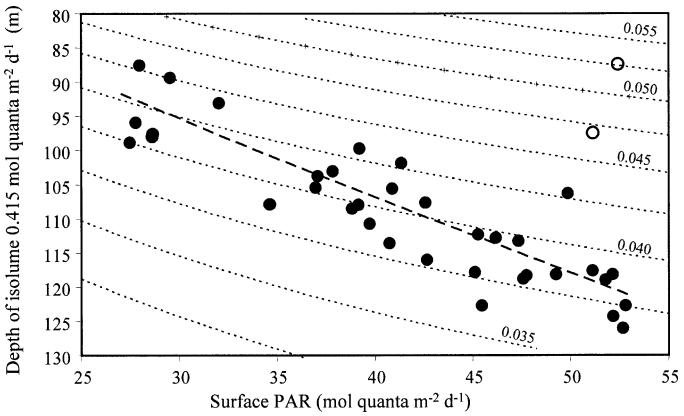


Fig. 5. Measured depth of the 0.415 mol quanta m^{-2} d^{-1} isolume as a function of sea-surface PAR. The thick dashed line is the regression of the isolume depth versus surface PAR excluding the two open circles that correspond to summer bloom events. The thin dashed lines correspond to the depth of this isolume as a function of sea-surface PAR assuming different depth-constant water-column PAR attenuation coefficients (K_{PAR}).

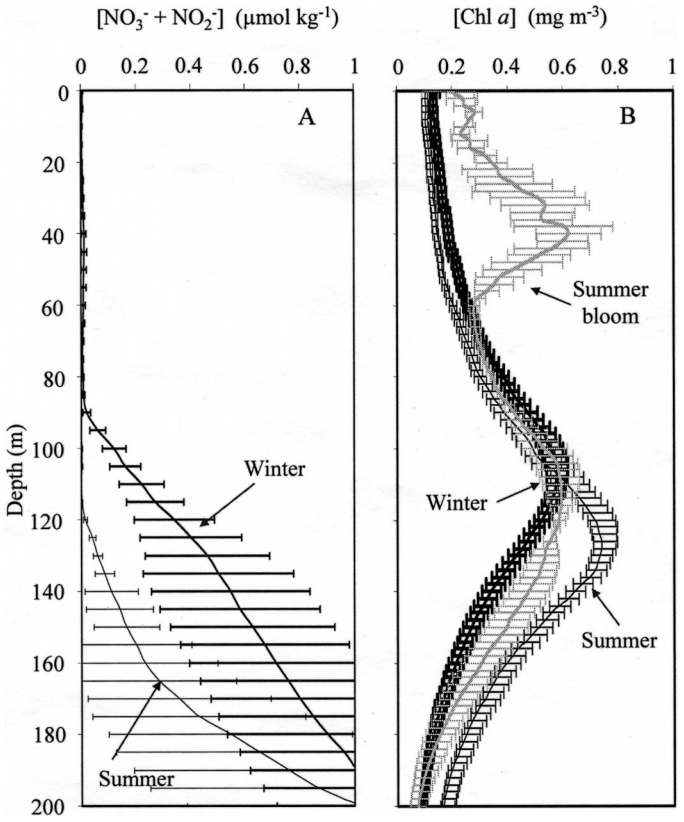


Fig. 6. Comparison of the average depth distribution of (A) $[NO_3^- + NO_2^-]$ and (B) chlorophyll for summer (thick line, surface PAR $<$ 30 mol quanta m^{-2} d^{-1}) and winter (thin line, surface PAR $>$ 48 mol quanta m^{-2} d^{-1}). Error bars correspond to the standard deviation. The average distribution of chlorophyll during summer bloom events for 1998 and 2000 is also included in panel B.

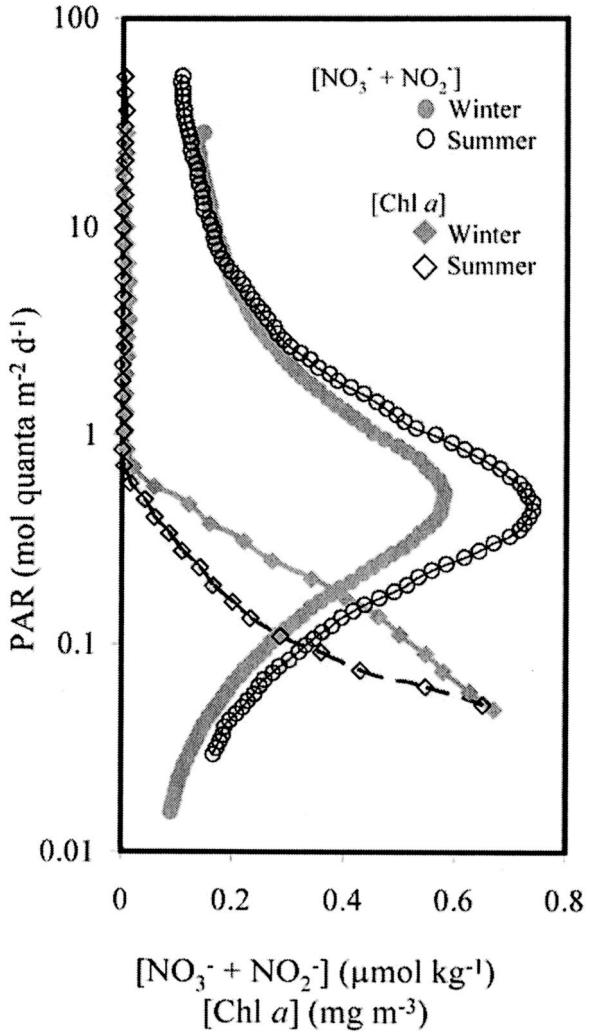


Fig. 7. Winter (gray) and summer (black) vertical distribution of $[NO_3^- + NO_2^-]$ (diamonds) and chlorophyll (circles) as a function of PAR.

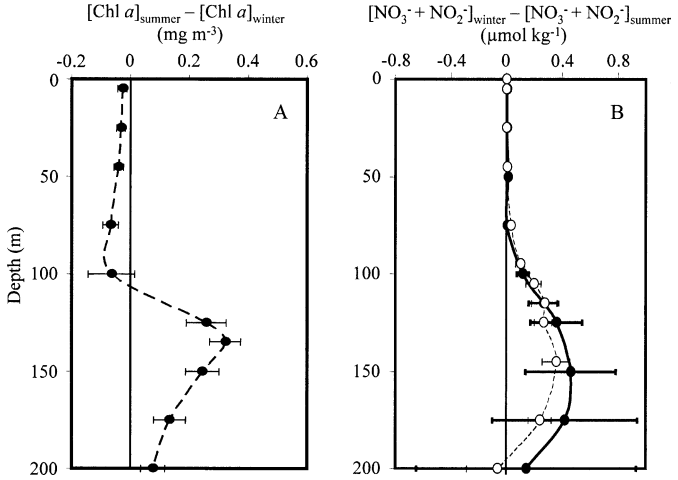


Fig. 8. Difference between the average distribution of (A) chlorophyll and (B) $[NO_3^- + NO_2^-]$ in winter and summer from January 1998 through December 2000. Open circles in panel B correspond to difference between winter and summer for the years 1989 through 1997.

than 15% of the observed nitrate depletion. Hence, although an increase in photoautotrophic biomass requires a certain degree of uncoupling between photosynthesis and grazing, our results suggest that most of the nitrate assimilated during spring and early summer is rapidly transferred to higher trophic levels or exported directly by gravitational processes acting on large phytoplankton cells.

In the context of photoautotrophic production, the amount of nitrogen needed to support the measured autotrophic organic carbon production at Station ALOHA is approximately 2 mol N m^{-2} yr^{-1} (Karl et al. 1997). On average, 9.5% of the integrated water-column autotrophic production takes place below 90 m. This fraction translates into a requirement of 0.19 mol m^{-2} to support the annual production below 100-m depth. Hence, the observed seasonal depletion of nitrate between 100- and 200-m depth accounts for approximately 20% of the production in this depth interval, as measured through ^{14}C in situ incubation techniques (Letelier et al. 1996).

A similar analysis can be made in terms of export production. The annual flux of nitrogen measured by drifting sediment traps positioned at 150-m reference depth is 106 mmol m^{-2} yr^{-1} (Karl et al. 1997). Hence, the seasonal nitrate depletion at the base of the euphotic zone measured between 1998 and 2000 accounts for approximately one-third of the measured export production. This seasonal depletion is also observed in the 1989 through 1997 HOT data set (Fig. 8B) and is consistent with the relative increase in heavy (nitrate-like) particulate nitrogen spring export observed by Dore et al. (2002). However, our calculation takes into account neither the organic nitrogen exported by vertical migrators and as dissolved matter nor the nitrate input into the lower euphotic zone through diffusion, the breaking of internal waves, and undetected deep mixing events. Furthermore, recent estimates of euphotic zone new production at Station ALOHA using the mass balance of oxygen and inorganic carbon suggest that free drifting sediment trap measurements may underestimate export fluxes in this oceanic region (Emerson et al. 1997).

The only other flux of new nitrogen estimated at Station ALOHA is that resulting from dinitrogen fixation. Although this estimate also has some large uncertainties, it is believed that dinitrogen fixation accounts for approximately 30–50% of the measured export production (Karl et al. 1997). From this perspective, the magnitude of the seasonal depletion of nitrate at the base of the euphotic zone is comparable to the annual estimates of dinitrogen fixation in the upper euphotic zone.

Because the top of the nitracline appears to oscillate seasonally between 90 and 120 m, it may be misleading to use a fixed depth horizon to estimate the availability of nitrate in the euphotic zone over time in regions of the ocean where the lower euphotic zone is almost permanently stratified. If we use the full HOT nutrient data record collected since 1988 and cluster the nitrate profiles into monthly bins, we observe a strong seasonal pattern in the 0–130-m integrated $[NO_3^- + NO_2^-]$ (Fig. 9). This pattern is closely correlated to

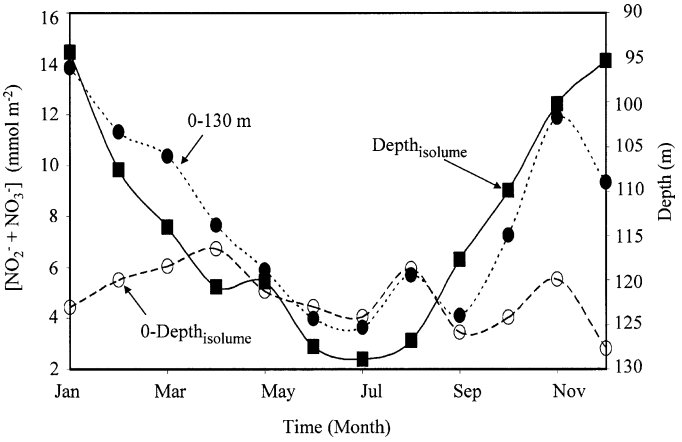


Fig. 9. Comparison of the average monthly integrated euphotic zone [NO_3^- + NO_2^-] using a constant depth horizon (0–130 m) and a constant isolume corresponding to the 129-m depth during the month of July (0.415 mol quanta m^{-2} d^{-1}). Filled circles = 0–130 m integration, open circles = integrated value from 0 m to the depth of the 0.415 mol quanta m^{-2} d^{-1} isolume, squares = depth of isolume 0.415 mol quanta m^{-2} d^{-1}.

the average depth position of the 0.415 mol quanta m^{-2} d^{-1} isolume, which is found at approximately 129 m during July. If, instead of integrating to a fixed depth, we integrate from surface to the depth of this isolume, then the seasonal pattern in [NO_3^- + NO_2^-] disappears. These results suggest that, although there is a larger concentration of nutrients between 100- and 130-m depth in winter, these nutrients may not be readily available to autotrophs due to the decrease in the average daily photon flux. They will become available only when they are displaced upward through physical processes or when isolumes start deepening during spring and early summer.

The nitracline light depth gradient below the 0.05 mol quanta m^{-2} d^{-1} isolume is not significantly different between winter and summer (Fig. 7), suggesting that below this light intensity (185 m in summer) the nutrient gradient is mainly driven by the balance between the degradation of organic matter, the potential heterotrophic use of inorganic nutrients, and upward diffusion. However, between this and the 0.7 mol quanta m^{-2} d^{-1} isolume we observe a deficit in summer nutrient concentration relative to winter. This temporal deficit of nutrients along isolumes may be the result of three distinct mechanisms: (1) a decrease in nutrient regeneration or diffusion or (2) an increased biological uptake along isolumes and (3) the upward migration of isolumes toward a shallower nitracline region.

Because neither the nitracline nor the pycnocline in the region between 185 and 300 m displays any significant seasonal differences, it is difficult to invoke a change in nutrient diffusion rates to explain the observed depletion along isolumes. The lack of seasonal estimates of nutrient regeneration rates at the base of the euphotic zone also precludes us from assessing the potential importance of this mechanism in explaining the observed seasonal differences.

An increase in biological nutrient uptake along isolumes can be attributed to the role of vertical migrating photoautotrophs under well-stratified water-column conditions. The potential for filamentous cyanobacteria to store energy through photosynthesis in the upper region of the water column and migrate at depth where nutrients are available has long been recognized in limnological studies (i.e., Fogg and Walsby 1971; Paerl and Tucker 1995). Karl et al. (1992) proposed that this mechanism could also be present in marine environments when water-column stratification selected for photoautotrophs with buoyancy control found at Station ALOHA. Under this scenario, energy stored by phytoplankton in the upper euphotic zone can be used in the upper nitracline for the uptake of nutrients. This process could potentially result in the removal of nutrients well below the isolume where photosynthesis equals community respiration, generating the observed summer depletion of nutrients along isolumes below the 0.7 mol quanta m^{-2} d^{-1} PAR level.

One caveat with this latter mechanism is the observation that all photoautotrophic taxa with buoyancy control identified to date in the NPSG have the direct or indirect capability to assimilate dinitrogen. Hence, the use of stored energy for the uptake of other forms of inorganic nitrogen in the nitracline may appear as a waste of energy. However, Villareal et al. (1993) have presented evidence suggesting that, in certain instances, the mat-forming diatom *Rhizosolenia* uses nitrate assimilated in the upper nitracline as the primary nitrogen source.

Lastly, the upward migration of isolumes without a concomitant nitrate increase at depth as an explanatory mechanism implies that during summer months the increase in nutrient concentration in the upper nitracline as a result of diffusion and nutrient regeneration is slower than the seasonal decrease in PAR due to the shoaling of isolumes. This interpretation is consistent with the observed uncoupling between the nitracline position and isolumes during summer bloom events. However, the rate of the vertical migration of an isolume caused by a summer bloom is significantly higher than that resulting from the seasonal cycle of surface PAR and K_{PAR}.

In order to compare the extreme summer and winter solar irradiance conditions, summer bloom events have been considered as special cases in the present study. However, there is ample field evidence suggesting that these bloom events are a recurrent phenomenon that can be observed at Station ALOHA under well-stratified water-column conditions. These short-lived events affect the light distribution in the euphotic zone (Figs. 3C and 5) and contribute significantly to the annual export production (Karl et al. 1996; Scharek et al. 1999*a*,*b*). During the first year of the HOT program a large surface bloom of the dinitrogen fixing cyanobacterium *Trichodesmium* was observed at Station ALOHA in August (Karl et al. 1992). Since then, the signature of summer cyanobacteria and diatom blooms has been observed in sediment traps during 1992 and 1994 (Karl et al. 1996; Scharek et al. 1999*a*,*b*) and in the pigments and irradiance depth distribution during 1995, 1998, and 2000 (Brzezinski et al. 1998; Fig. 4). The dominant species detected during these summer bloom events have in common their capacity to regulate buoyancy (Walsby 1978; Villareal et al. 1993, 1999). Furthermore, while *Trichodesmium* fixes dinitrogen (Letelier and Karl 1998 and references therein), the dominant diatom

species responsible for summer blooms can carry the endosymbiotic dinitrogen-fixing cyanobacterium *Richelia intracellularis* (Heinbokel 1986). The nitrogen isotope signature of particulate material collected in the sediment traps at HOT indicates that these summer blooms are largely supported by dinitrogen fixation (Karl et al. 1997; Dore et al. 2002).

As observed in Figs. 3C and 5, these summer blooms strongly affect the light distribution in the upper water column. It is during these events that the highest mean water-column K_{PAR} has been observed (surface 1% K_{PAR} = 0.0525 m^{-1} in August 1998; Fig. 5), forcing isolumes to shoal 35 m relative to seasonally matched nonbloom conditions. During the sampling of the 1998 summer bloom event, the mean DCML position was observed in the vicinity of the 0.5 mol quanta m^{-2} d^{-1}. This position is not different than that found during nonbloom events. However, the top of the nitracline was significantly deeper than that observed during nonbloom conditions (0.15 mol quanta m^{-2} d^{-1}). This result suggests that although the position of the DCML responds on the order of days to the decrease in photon flux at depth, the diffusion of nutrients into the lower euphotic zone is a significantly slower process. Similar conclusions regarding temporal scales of displacement of the nitracline and the DCML were reached by Cullen and coworkers when analyzing high-resolution time series of nearshore vertical motion of Chl *a*, nitrate, and temperature on the Southern California shelf (Cullen et al. 1983).

Finally, from an ecological perspective it may be of interest to speculate on the effect that a seasonal deepening and shoaling of isolumes may have in the community structure found in the permanently stratified region of the euphotic zone. Assuming that the mean vertical displacement of isolumes follows the seasonal sea-surface cycle of solar irradiance, we can calculate the theoretical depth penetration velocity of a particular isolume at any time of the year. Using the nitrate gradient observed during winter months (Fig. 7) and the maximum rate of isolume depth penetration (0.3 m d^{-1}), we calculate that isolumes in the upper nitracline will experience a maximum increase in $[NO_3^- + NO_2^-]$ of approximately 3.5 nmol kg^{-1} d^{-1} during the spring season. This injection of new nitrogen into an isolume can be translated into the production of organic matter at a rate of approximately 0.3 mg C m^{-3} d^{-1}. This amount corresponds to approximately 36% of the average spring photoautotrophic production measured at 125-m depth at Station ALOHA. In contrast, the autumn period will experience a steady retreat of the isolumes from the nitracline at a maximum rate of 0.3 m d^{-1}. Hence, during this autumn period we should expect a shift in the phytoplankton assemblage toward ammonium or dissolved organic nitrogen-based production.

John Ryther's warning statement regarding his working definition of euphotic zone (Ryther 1956) implicitly recognizes that the definition will depend on the question being addressed. The integrated photautotrophic production below the 1% surface PAR level at Station ALOHA accounts for less than 8% of the total water-column integrated production, well within the uncertainty of the ^{14}C measurement (Letelier et al. 1996). However, if our aim is to understand the processes driving new and export production in this pelagic environment, we may need to define the euphotic zone in reference to isolume depths (*see also* Siegel et al. 2002). The present study documents a light driven seasonal cycle in the lower euphotic zone at Station ALOHA. This cycle is characterized by a significant deepening of the DCML and the upper nitracline and a concomitant increase in the magnitude of the DCML during spring and summer. Although our conceptual perspective of the North Pacific subtropical gyre is that of an environment with only sporadic and short-lived bloom events, the seasonal increase in phytoplankton biomass in the lower euphotic zone appears to have all the basic characteristics of a spring bloom event. The main difference when compared to our traditional view of a spring bloom is that the observed increase in biomass is moderate and remains restricted to the base of the euphotic zone, away from the sight of a sea level ship-based observer or an orbiting satellite-based sensor. Nevertheless, this seasonal increase is driven by an increase in light availability and the supply of nutrients at depth, having the potential to contribute significantly to the depth-integrated water-column annual new production.

Harald Sverdrup's critical depth concept (Sverdrup 1953) defined the water-column conditions necessary for the development of a spring bloom in the mixed layer. The fundamental hypothesis in his seminal paper stated that the spring bloom will take place when the depth of the mixed-layer shoals above the depth at which water-column integrated photosynthesis equals water-column respiration. In a recent paper Siegel et al. (2002) pointed out two of the main assumptions underlying Sverdrup's hypothesis: (1) the lack of nutrient limitation in the euphotic zone and (2) the lack of heterotrophs. The results of Siegel and coauthors indicate that the spring bloom in the North Atlantic takes place only when the environmental conditions allow photoautotrophic production to exceed respiration. Sverdrup's model works in areas where the mixed-layer community is limited by light during the winter–spring transition. However, this model does not explain the observed biological dynamics in areas where the community is limited by nutrients rather than light.

Both Sverdrup (1953) and Siegel et al. (2002) focus their attention on the dynamics in the upper euphotic zone of oceanic regions where winter mixing erodes the upper nutricline. Although the results of Siegel and coauthors may be extrapolated to pelagic ecosystems where the upper nutricline is under permanent stratification, their study does not address the ecosystem dynamics in the lower region of the euphotic zone. In this context, the data collected by the HOT program are of great value. They suggest the presence of a seasonal cycle in the phytoplankton assemblage along isolumes (Fig. 7a) and a partial uncoupling between photosynthesis and respiration that translates into an increase of the DCML magnitude in summer, relative to winter.

Hence, the euphotic zone at Station ALOHA can be divided into an upper region (0–90 m) that is almost permanently under nutrient limiting conditions (sensu Liebig 1840) and a lower region (90–200 m) that exhibits a seasonal cycle and may support an annual phytoplankton succession pattern. This division is consistent with the two-layered euphotic zone conceptual model of the North Pacific oligotrophic

gyre that resulted from the VERTEX (Vertical Transport and Exchange) time-series study (Coale and Bruland 1987; Small et al. 1987). It is also consistent with the historical observations by E. Venrick in the North Pacific that established the presence of distinct phytoplankton assemblages in the upper and lower euphotic zone (Venrick 1988).

Although bloom events in the upper euphotic zone have been observed in this oceanic region, they are short lived and stochastic in nature. Furthermore, they are induced by various dissimilar processes that can take place in different seasons, such as storm events (Ditullio and Laws 1991), the passage of eddies (Letelier et al. 2000; Seki et al. 2001), and the activity of photoautotrophic assemblages characterized by the capacity to assimilate dinitrogen and control their buoyancy under well-stratified summer conditions (Karl et al. 1992; Brzezinski et al. 1998). Although changes in the photoautotrophic assemblage have been reported for these events, it is not known whether they generate consistent succession patterns and how important they are in supporting the observed microbial diversity. In contrast, the seasonal interaction between light and nutrient availability in the lower euphotic zone appears to be a consistent and recurrent mechanism that can control and support biological diversity in these depth strata.

The amplitude of the sea-surface PAR seasonal cycle will increase with latitude, amplifying the depth range oscillation of isolumes. For this reason we could expect an even stronger interaction between isolume depth and nutrients at higher latitudes. Yet, the increase in phytoplankton biomass during spring blooms, the frequency of deep mixing events, and the increase in water-column instability can all contribute to confound or preclude the development of a seasonal cycle in the lower euphotic zone at higher latitudes.

Although it may be difficult to extrapolate our results to higher latitudes, we submit that the seasonal changes that we describe herein may be common in tropical and subtropical oceanic oligotrophic habitats. As such, they represent >30% of the Earth's surface and may be a dominant biome on the surface of our planet. Furthermore, the HOT observations discussed in this paper may help us understand the evolution of pelagic environments and their role in biogeochemical cycles under a climate change scenario. If an increase in the upper water-column density gradient forces the permanent stratification of the upper nutricline in subtropical pelagic environments, we should expect a rise in the contribution to new and export production by the lower euphotic zone community and by vertical migrating photoautotrophic assemblages.

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