

Light limitation of summer primary production in the coastal Gulf of Alaska: physiological and environmental causes

Suzanne L. Strom*, Erin L. Macri, Kerri A. Fredrickson

Shannon Point Marine Center, Western Washington University, 1900 Shannon Point Road, Anacortes, Washington 98221, USA

ABSTRACT: We examined photosynthesis–irradiance (P - E) relationships for coastal Gulf of Alaska phytoplankton communities during summer 2003. Phytoplankton were adapted to high light levels, with elevated light saturation parameters (average E_k 390 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), low photosynthetic efficiencies (α), and an absence of photoinhibition. Maximum photosynthesis rates (P_{max}) ranged from 0.9 to 12.9 $\mu\text{g C } \mu\text{g chl a}^{-1} \text{h}^{-1}$ and were consistently higher in the nearshore Alaska Coastal Current than elsewhere in the region. Differences between photosynthetic responses of phytoplankton communities from near surface versus the subsurface chlorophyll maximum layer were minor. Small phytoplankton ($<20 \mu\text{m}$) had consistently higher P_{max} and α -values than did large phytoplankton ($>20 \mu\text{m}$), a difference associated with the higher C:chlorophyll ratios of the small phytoplankton. Acclimation to high light probably arose because of the shallow pycnocline and the highly variable light environment, the latter generated by internal waves and variable cloud cover. Simulations showed that estimated water column productivity, which ranged from 359 to 909 $\text{mg C m}^{-2} \text{d}^{-1}$, was sensitive to modeled changes in cloud cover and pycnocline depth, through both direct effects on light availability and indirect effects on phytoplankton physiology. Climate change could therefore affect summer primary production rates in the coastal Gulf of Alaska through changes in stratification, wind mixing energy, and cloud cover. However, summer phytoplankton growth in this region is also limited by nutrient availability and microzooplankton grazing, indicating a potentially complex relationship between phytoplankton production and environmental variability.

KEY WORDS: Photosynthesis · Irradiance · Phytoplankton · Subsurface chlorophyll maximum

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INTRODUCTION

The northern coastal Gulf of Alaska (CGOA) is a productive ecosystem supporting high abundances of fish, shellfish, seabirds and marine mammals. Annual yields of numerous fish and shellfish stocks are linked with variations in climate conditions, including the Pacific Decadal Oscillation (PDO) in the North Pacific basin (Beamish & Bouillon 1993, Hollowed et al. 2001). The US Global Ocean Ecosystem Dynamics (GLOBEC) Northeast Pacific program was designed to explore these linkages, with a focus on the continental shelf as an area where Pacific salmon *Oncorhynchus* spp. experience a critical period for survival and growth (Cross et al. 2008 and references therein). Variations in

primary production, leading to qualitative and quantitative changes in shelf food webs, are clearly one mechanism by which climate fluctuations could translate into variable abundances of higher trophic-level organisms such as salmon. For example, the 'optimal window of stability' hypothesis (Gargett 1997) proposed that primary production in the CGOA is primarily limited by availability of light (as opposed to nutrients); therefore, reductions in wind-mixing energy should generally lead to higher production through shoaling of the mixed layer and increased light exposure of phytoplankton therein.

To test hypotheses such as these, we need data on the magnitude of primary production in the CGOA and its relationship with environmental variation. At pre-

*Email: suzanne.strom@wwu.edu

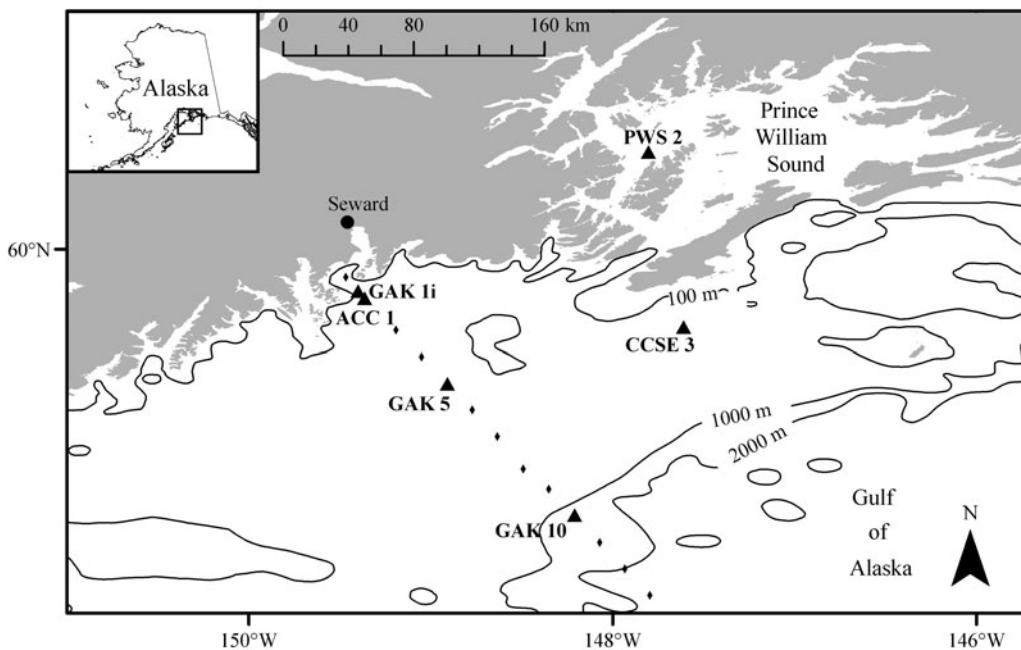


Fig. 1. Study region in northern Gulf of Alaska showing all Seward Line stations GAK-1 through GAK-13 (small diamonds), as well as all stations (labeled triangles) for which data are presented in this paper

sent, there are few published primary productivity measurements for the region (Sambrotto & Lorenzen 1986). Furthermore, weather and climate patterns in the northern CGOA are not clearly tied to basin-scale variations such as the Pacific Decadal Oscillation (Stabeno et al. 2004), so understanding linkages between climate and higher trophic levels in that ecosystem requires regional data collection and modeling. As part of our investigation of the regulation of phytoplankton growth and production in the CGOA, we conducted a series of photosynthesis–irradiance (*P-E*) experiments during summer 2003 in the US GLOBEC study area (Fig. 1), encompassing Prince William Sound and the continental shelf and slope offshore from Resurrection Bay and Seward, Alaska. The northern Gulf of Alaska is a high-energy environment where physical and biological oceanographic processes are driven by a combination of strong wind events, high amounts of freshwater runoff, large tidal exchanges and the passage of mesoscale eddies (Stabeno et al. 2004). The buoyancy- and wind-driven Alaska Coastal Current (ACC) flows westward close to the coast; the mid-shelf is characterized by weaker and more directionally variable flows; while the westward-flowing Alaska Current occupies the outer shelf–slope region. Winter winds drive strong downwelling, while weaker upwelling episodes can occur during summer. Also during summer, the shelf becomes stratified by warming surface waters and, nearshore, by freshwater inputs (Weingartner et al. 2005). Nutrient depletion of surface waters is observed as early as May and leads to nitrogen-limited phytoplankton growth throughout

much of the summer (Childers et al. 2005, Strom et al. 2006); there is also evidence for reduced iron availability and episodic iron limitation of phytoplankton growth on the mid- and outer shelf in the Seward region (Strom et al. 2006, Wu et al. 2009).

We conducted *P-E* experiments in a paired manner so that surface mixed layer and subsurface chlorophyll maximum (SCM) communities could be evaluated simultaneously at each station. Our goals for the study were to (1) assess primary productivity during the summer season of strong stratification; (2) evaluate photosynthetic performance as a function of geographic location, depth and phytoplankton size class; and (3) make predictions regarding the sensitivity of the phytoplankton community to light limitation. With *P-E* and accompanying oceanographic data, we were able to examine some aspects of environmental variation, including fluctuations in cloud cover and mixed layer depth. Both *P-E* data and these simple model explorations demonstrated that the summer 2003 phytoplankton community was vulnerable to light limitation, as a consequence of both environmental conditions and phytoplankton photophysiology.

MATERIALS AND METHODS

Hydrographic measurements were made with a Seabird SBE 9/11 Plus CTD system. The instrument package also contained a Biospherical Instruments QSP200L spherical sensor for photosynthetically active radiation (PAR, $\mu\text{mol photons m}^{-2} \text{s}^{-1}$), and a Seatech

FL0500 submersible fluorometer for detection of *in situ* chlorophyll *a* (chl *a*) fluorescence. Incident irradiance (E_0) was measured continuously by a Li-Cor 2π PAR sensor mounted on the ship's superstructure.

Water samples for P - E experiments were collected using 5 l Niskin bottles with external spring closures on the CTD rosette. In all but 2 cases, P - E relationships were determined for 2 depths at each station (Fig. 1), one corresponding to 50% surface irradiance (50% E_0) and the other to the SCM. The former ranged from 4 to 9 m and the latter from 15 to 23 m. Water from each depth was subsampled into eleven 300 ml polycarbonate bottles, each of which was inoculated with 0.04 ml (10 μ Ci) 14 C-labeled sodium bicarbonate (Moravek Biochemicals). Average total activity was determined by subsampling (0.1 ml) 4 haphazardly selected bottles and adding each subsample to 4 ml Ecoscint scintillation cocktail buffered with 0.4 ml 0.1 M NaOH. Bottles were screened with neutral density filters (Kodak Wratten) to achieve a gradient in light intensity from 100 to 2% E_0 ; a dark bottle was also included. Bottles were incubated for 6 h in a Plexiglas incubator cooled by flowing surface seawater. All incubations were initiated between 08:30 and 10:45 h local time (note that local apparent noon was at \sim 13:00 h). Experiments were terminated by dividing the contents of each bottle into 2 portions, measuring the volume of each (\sim 150 ml), and then filtering one through a 25 mm glass fiber filter (0.7 μ m nominal pore size) and the other through a 25 mm polycarbonate filter with 20 μ m pore size. Filters were placed in 20 ml plastic scintillation vials with 0.5 ml 0.5 N HCl and allowed to acidify in a fume hood for 24 h. Scintillation cocktail (10 ml) was then added to each vial and disintegrations per minute (dpm) were determined using a Packard Tri-Carb 1900TR liquid scintillation analyzer. Samples were counted immediately on board the research vessel and again at Shannon Point Marine Center after several weeks of dark storage; results were essentially identical. For each vial, dpm values were converted to photosynthesis rates (μ g C ml^{-1} h^{-1}) after subtraction of dark uptake, according to Parsons et al. (1984).

Samples for estimation of chl *a* concentration were taken in triplicate from the same 5 l Niskin bottles used to fill the P - E incubation bottles. Duplicate samples for floristic analysis (see Strom et al. 2006 for methods) were taken at the same time. Each chl *a* sample was filtered through a fractionation cascade containing a 20 μ m pore size polycarbonate filter over a glass fiber filter (0.7 μ m nominal pore size). Samples were extracted in 90% acetone for \sim 24 h at -20°C and chl *a* concentration determined fluorimetrically (Turner 10-AU) using the acidification method (Welschmeyer 1994). Photosynthesis rates were normalized to chl *a* concentration in the appropriate size fraction to yield

biomass-specific rates (P^B , μ g C μ g chl a^{-1} h^{-1}) for further analysis.

For estimation of photosynthetic parameters, values of P^B and the corresponding irradiance (E) were fit to the hyperbolic tangent function of Jassby & Platt (1976):

$$P^B = \tanh\left[\frac{\alpha E}{P_{\max}}\right] \quad (1)$$

where α is photosynthetic efficiency and P_{\max} is maximum chlorophyll-normalized photosynthesis rate. Curve fits were done in SigmaPlot 2002 for Windows v. 8.02 using the Marquardt-Levenberg algorithm. Convergence was defined as a tolerance of 0.0001. The saturating irradiance for photosynthesis (E_k) was calculated from P_{\max}/α . E_k represents the optimal irradiance for photosynthesis (Sakshaug et al. 1997). Curve-fitting and parameter estimation was done separately for <20 and >20 μ m phytoplankton. No term for photoinhibition was included because we saw no evidence for photoinhibition in the data.

Euphotic zone attenuation coefficients (k , m^{-1}) were derived from the slope of ln-transformed subsurface PAR profiles. Separate k values were determined for the surface mixed layer (k_{surf}) and the SCM layer (extending from the top of the SCM to the bottom of the euphotic zone; k_{SCM}). Estimation was done iteratively so that only euphotic zone depths (i.e. to 1% E_0) were included in the calculation of k . Irradiance (E_z , $\mu\text{mol photons m}^{-2}$ h^{-1}) at each meter depth (z) and for each hour of the day was predicted from k values and incident irradiance (E_0) according to $E_z = E_0 e^{-k_{\text{surf}} \Delta z}$ for depths above the SCM, and $E_z = E_{\text{SCM}} e^{-k_{\text{SCM}} \Delta z}$, where E_{SCM} is irradiance at the top of the SCM layer, for depths below the top of the SCM.

Chlorophyll at each meter depth was estimated from algorithms comparing extracted chl *a* concentrations (total) with *in situ* fluorescence. These algorithms were developed from noon CTD casts done on the same day (i.e. within several hours) and at the same station as casts for P - E experiments. Samples for extracted chl *a* were taken at 10 depths within and just below the euphotic zone and processed as described for P - E chl *a* samples. Linear relationships between total extracted chl *a* and *in situ* fluorescence for each cast provided a good fit to the data ($r^2 \geq 0.87$). These relationships, along with the average fraction of total chl *a* in the >20 μ m size class, were used to predict chl $_{>20}$ and chl $_{<20}$ at each meter depth from 1 m averaged *in situ* fluorescence profiles collected during morning P - E casts. No predictive relationship between extracted chl *a* and *in situ* fluorescence could be developed for station GAK-10. Here we saw no evidence for a SCM and used a simple extrapolation of extracted chl *a* values to predict chl $_{>20}$ and chl $_{<20}$ at each meter depth.

Samples for nitrate and silicic acid analyses were taken from the same noon casts used to develop fluorescence versus extracted chl *a* relationships (see Strom et al. 2006 for methods).

Integrated daily water column primary production was estimated from the sum of $P_{<20}$ and $P_{>20}$ in each cubic meter of the euphotic zone according to:

$$P_{>20} = \text{chl}_{>20} P_{>20}^B = \text{chl}_{>20} \tanh \left[\frac{\alpha_{>20} E}{P_{\max >20}} \right] \quad (2)$$

where $\text{chl}_{>20}$ is the concentration of chl *a* (mg m^{-3}) in the $>20 \mu\text{m}$ size fraction and $P_{>20}$ is the volume-normalized primary productivity in the $>20 \mu\text{m}$ phytoplankton size fraction ($\text{mg C m}^{-3} \text{h}^{-1}$). Analogous calculations were done for $P_{<20}$. To estimate daily production, measured rates were divided by incubation time (h); hourly rates were then scaled to each hour's irradiance at each euphotic zone depth. Integrated daily primary production (P_{INT} , $\text{mg C m}^{-2} \text{d}^{-1}$) was then determined as the sum of hourly primary production in both chl *a* size fractions over the euphotic zone. Direct estimates of P_{INT} were based on *P-E* parameters collected during that day at that station. In some cases we applied *P-E* parameters from a nearby station in the same shelf

region to another day and location to derive indirect estimates of P_{INT} .

RESULTS

Photosynthetic parameters

For experiments in which it could be estimated, P_{\max} ranged from 0.9 to 4.9 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ for large ($>20 \mu\text{m}$) phytoplankton, and from 2.9 to 12.9 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ for small ($<20 \mu\text{m}$) phytoplankton (Table 1). Photoinhibition was never observed. Photosynthetic efficiency (α) for large phytoplankton ranged from 0.003 to 0.016 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ and for small phytoplankton from 0.012 to 0.033 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Table 1). P_{\max} and α were uncorrelated. The light saturation parameter (E_k) ranged from 190 to 940 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ across both size classes.

P-E experiments were conducted in paired fashion to investigate differences between near-surface (mixed layer) and SCM communities. Contrary to expectation, there were no significant differences between the 2

Table 1. Sampling data, sea surface (i.e. incubation) temperature (T), total incident irradiance received during 6 h experiments (E_0 , $\text{mol photons m}^{-2}$), initial chl *a* levels (total [$\mu\text{g l}^{-1}$] and fraction $>20 \mu\text{m}$ [frac >20]) and photosynthetic parameters estimated from *P-E* relationships for experiments conducted during summer 2003 in the coastal Gulf of Alaska. P_{\max} : maximum (light saturated) biomass-specific photosynthetic rate ($\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$); α : photosynthetic efficiency ($\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); E_k : saturating irradiance for photosynthesis ($\mu\text{mol photons m}^{-2} \text{ s}^{-1}$); nd: not determined due to insufficient light for saturation of photosynthetic response

Date	Station	Depth (m)	T (°C)	E_0	Chl <i>a</i>		P_{\max}		α		E_k	
					($\mu\text{g l}^{-1}$)	frac >20	$>20 \mu\text{m}$	$<20 \mu\text{m}$	$>20 \mu\text{m}$	$<20 \mu\text{m}$	$>20 \mu\text{m}$	$<20 \mu\text{m}$
21 Jul	GAK-10	6	13.9	22.3	0.69	0.17	2.26	2.95	0.010	0.015	220	200
		17		26.9	0.60	0.15	2.77	4.58	0.008	0.019	330	240
23 Jul	GAK-10	9	13.9	12.4	0.54	0.19	nd	nd	0.005	0.017	nd	nd
		18		13.3	0.62	0.18	3.03	5.37	0.010	0.020	300	270
25 Jul	PWS-2	4.5	14.7	6.2	0.43	0.44	nd	nd	0.007	0.026	nd	nd
		21		7.3	1.41	0.18	nd	nd	0.007	0.024	nd	nd
27 Jul	PWS-2	5	14.7	15.0	0.45	0.17	2.05	6.85	0.007	0.025	310	280
		21		19.1	1.25	0.15	1.36	3.75	0.005	0.019	300	190
29 Jul	ACC-1 ^a	4	14.2	16.5	0.75	0.52	nd	nd	0.010	0.021	nd	nd
		19		16.6	1.05	0.39	nd	nd	0.016	0.019	nd	nd
1 Aug	GAK-1i ^a	5	14.2	29.2	0.49	0.54	4.14	10.59	0.008	0.024	530	450
2 Aug	ACC-1 ^a	4	14.3	29.1	0.39	0.49	4.93	11.43	0.006	0.012	810	940
		18		27.0	2.36	0.71	3.88	12.89	0.007	0.023	520	560
4 Aug	GAK-5	5	14.6	24.8	0.30	0.13	3.06	6.78	0.005	0.012	570	550
		23		28.1	1.55	0.09	0.90	7.01	0.003	0.021	280	330
6 Aug	GAK-5	5	14.6	9.8	0.39	0.10	nd	nd	0.007	0.017	nd	nd
		15		10.7	1.58	0.08	1.92	8.77	0.007	0.033	280	260
9 Aug	CCSE-3 ^a	4	15.0	16.4	0.68	0.48	nd	nd	0.011	0.020	nd	nd
10 Aug	GAK-5	5	14.6	7.8	0.30	0.13	nd	nd	0.009	0.018	nd	nd
		15		9.5	1.29	0.05	nd	3.68	0.004	0.019	nd	200

^aConsidered Alaska Coastal Current (ACC) station

depths in either P_{\max} or α , for either large or small phytoplankton (paired t -test, all p -values > 0.18). Therefore, P_{\max} and α data from the 2 depths were pooled for all subsequent analyses (see next paragraph). The light saturation parameter (E_k) also did not differ significantly between the surface and SCM (paired t -test, $p = 0.18$ for large phytoplankton, $p = 0.10$ for small phytoplankton). However, when it could be estimated for both depths simultaneously, E_k was lower in the SCM than in near-surface samples in every case except Station GAK-10, which did not have a true SCM (Table 1). Furthermore, P - E curves for SCM phytoplankton reached light saturation in most instances (i.e. on 13 of 18 dates and chl a size fractions), while curves for near-surface phytoplankton, incubated under the same light regimes, reached saturation less than half the time (10 of 22 dates and size fractions). Thus, although P_{\max} and α did not differ systematically between depths, there was a strong tendency for photosynthesis rates to saturate at a lower irradiance in the SCM than in the near-surface community.

The effects of phytoplankton size and experiment location were examined using 2-way ANOVA. Phytoplankton size class had a major effect on photosynthetic performance (Fig. 2). Small phytoplankton had significantly higher P_{\max} values than large phytoplankton (average 7.1 vs. 2.8 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$, $p < 0.001$), as well as significantly higher photosynthetic efficiencies (average 0.020 vs. 0.008 $\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, $p < 0.001$). In contrast, phytoplankton size did not affect E_k ($p = 0.585$) (Fig 2C). Location influenced P_{\max} and E_k ($p \leq 0.001$), but not α ($p = 0.578$). Phytoplankton in the Alaska Coastal Current (ACC) had P_{\max} and E_k levels approximately twice as high as those elsewhere, while parameters did not vary among other regions (Tukey's HSD pairwise comparisons, Fig. 2). There were no significant interactions between size class and location for any photosynthetic parameter.

Estimated water column productivity

We estimated integrated water column productivity at the 4 stations for which we obtained a complete set of photosynthetic parameter estimates at both depths. Values ranged from 359 $\text{mg C m}^{-2} \text{ d}^{-1}$ at slope station GAK-10 to 748 $\text{mg C m}^{-2} \text{ d}^{-1}$ at an ACC station (Table 2). To estimate the possible maximum productivities at this time in this region, we applied photosynthetic rates from nearby stations to measured chl a profiles and daily incident irradiance levels at 2 high-chl stations, GAK-1i and HE-2 (Fig. 1). Although integrated chl a concentrations were similar at the 2 sta-

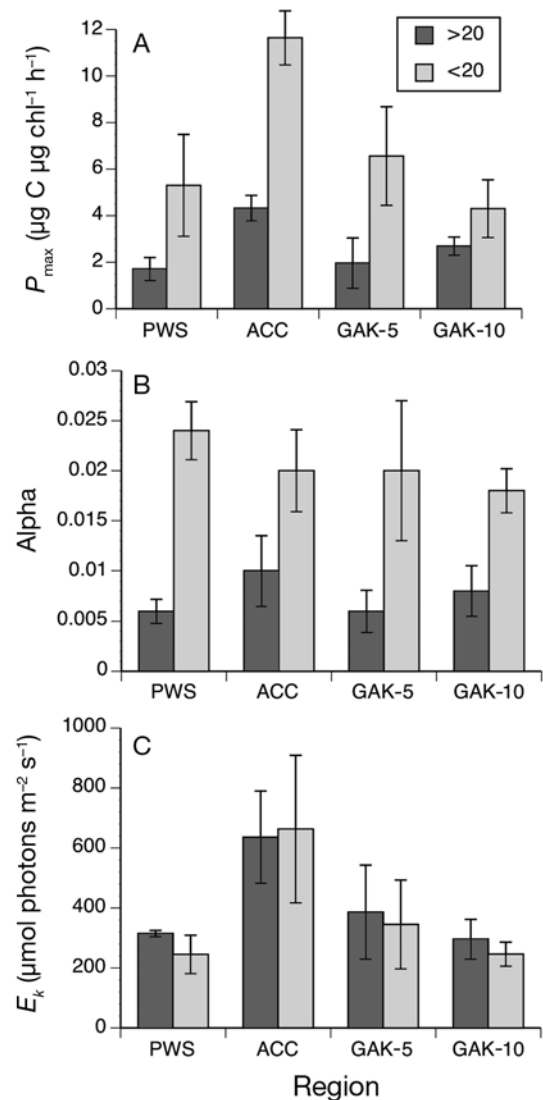


Fig. 2. Photosynthetic parameters from P versus E experiments, including (A) maximum photosynthetic rate (P_{\max}), (B) photosynthetic efficiency, or α , ($\mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and (C) light saturation parameter (E_k). Values are average \pm SD for phytoplankton cells $>20 \mu\text{m}$ (dark grey bars) and $<20 \mu\text{m}$ (light grey bars) for experiments conducted in 4 different regions of the coastal Gulf of Alaska. PWS: Prince William Sound; ACC: Alaska Coastal Current; GAK-5: mid shelf; GAK-10: shelf break

tions, HE-2 yielded a higher daily production estimate (909 vs. 617 $\text{mg C m}^{-2} \text{ d}^{-1}$, Table 2).

Small ($<20 \mu\text{m}$) phytoplankton were the major contributors to primary production during this summer sampling period in the CGOA. Small phytoplankton comprised most of the total chl a at most stations and depths (Table 1). In addition, their higher chl-specific photosynthesis rates meant that the small phytoplankton contribution to total production substan-

Table 2. Summer 2003 water column chl *a* and primary production (PP) (integrated daily total [Int] and percent in cells > 20 μm [% > 20]) as estimated from *P-E* parameters (see 'Materials and methods' for details). Integration was to the base of the euphotic zone (depth of 1% surface irradiance). E_0 : daily incident irradiance ($\text{mol photons m}^{-2}$); k : attenuation coefficients (m^{-1}) for the surface mixed layer/subsurface chlorophyll maximum layer; Z_{eu} : euphotic zone depth (m); Int chl *a* (mg m^{-2}); Int PP ($\text{mg C m}^{-2} \text{d}^{-1}$)

Date	Station	E_0	k	Z_{eu}	Chl <i>a</i>		PP	
					Int	% > 20	Int	% > 20
Direct								
21 Jul	GAK-10	37.9	0.15/0.09	41	24.8	17	359	12
27 Jul	PWS-2	32.8	0.14/0.09	42	26.6	21	581	7
2 Aug	ACC-1	49.3	0.12/0.15	34	35.3	38	748	27
4 Aug	GAK-5	50.7	0.14/0.15	32	34.5	9	524	3
Indirect								
1 Aug	GAK-11	43.2	0.11/0.11	41	38.6	45	617	28
8 Aug	HE-2	37.4	0.07/0.19	24	36.2	77	909	54

Table 3. Partitioning of daily primary production (PP, $\text{mg C m}^{-2} \text{d}^{-1}$) and chl *a* (mg chl a m^{-2}) into surface and subsurface chlorophyll maximum (SCM) layers at 3 stations in the coastal Gulf of Alaska. Depth-integrated values for each layer are shown, as well as their percent contribution to the integrated euphotic zone totals (% of total)

Station Date (2003)	Layer	Depth range (m)	PP	% total	Chl <i>a</i>	% total
PWS-2 27 Jul	Surface	0–11	453	78	8.9	33
	SCM	12–29	128	22	14.9	56
ACC-1 2 Aug	Surface	0–12	437	58	8.4	25
	SCM	13–24	298	40	17.0	50
GAK-5 4 Aug	Surface	0–13	299	57	6.1	17
	SCM	14–35	225	43	29.8	83

tially exceeded their contribution to total chl *a* biomass (Table 2). Even at station HE-2, which was dominated (77%) by large cells, small phytoplankton contributed nearly half of the estimated daily integrated production.

We assessed the contribution of the SCM to water column productivity for 3 of the 4 stations with complete *P-E* data (note that station GAK-10 did not exhibit a true SCM). Although the SCM is a striking and widespread feature of the summer shelf (Fig. 3), this feature is of variable importance to water column production. At mid-shelf Station GAK-5, close to half of the integrated production was in the SCM (Table 3), while most of the integrated chl *a* was in this feature. Overall, although the SCM could account for a significant proportion of the total chl *a*, the surface mixed layer was still the most important production zone, contributing more than 50% of the integrated total at all 3 stations (Table 3).

Effects of environmental variation on primary production

The high incidence of unsaturated *P-E* relationships obtained in this study (Table 1) demonstrates that summer irradiance was likely to be limiting to photosynthesis on numerous occasions in the CGOA, even in surface waters. Comparison of E_k values with midday irradiance levels taken over a 6 h period showed that, based on the study-wide average E_k of $10.6 \text{ mol photons m}^{-2} \text{ h}^{-1}$, photosynthesis rates would have been below saturation (i.e. less than P_{max}) on 6 of 22 d during the cruise period, even at the sea surface (Fig. 4A). We investigated this phenomenon further by

estimating integrated daily production at Station ACC-1 over the range of observed irradiance levels. During our cruise period (21 July to 10 August), daily incident irradiance ranged widely, from a minimum of 8.2 to a maximum of $50.7 \text{ mol photons m}^{-2} \text{ d}^{-1}$ (15 to 91% of the maximum cloud-free irradiance of $56 \text{ mol photons m}^{-2} \text{ d}^{-1}$). Water column chl *a* levels and *P-E* parameters from station ACC-1 (2 August, Table 1) were used to estimate the effect of this variability on primary productivity. Integrated daily production rates were quite sensitive to observed variations in irradiance (Fig. 4B). Even modest irradiance decreases relative to the cloud-free condition caused some reduction; the cloudiest observed day (28 July) would have yielded an integrated daily production <20% of that realized on a cloud-free day.

Another factor that can influence irradiance availability and, hence, production is the depth of the SCM. We collected numerous *in situ* fluorescence profiles at mid-shelf Station GAK-5 during our cruise. These profiles reveal that the SCM depth varied between 11 and 27 m over an 8 d period in August, with an average of 21 m (Fig. 5A). Observations closely spaced in time (Fig. 5A inset) show that at least some of the variability occurred in wave-like oscillations, which was perhaps related to the passage of internal waves. Furthermore, the SCM tended to be shallower during the later part of the observation period (11 and 12 August). We simulated the effect of SCM depth variation on mid-shelf primary production by artificially relocating the observed GAK-5 (4 August) SCM layer so that the peak occurred at different depths. Because of the high light-adapted nature of the phytoplankton community, integrated water column productivity was strongly influenced by SCM depth, particularly near the shallower end of the observed range (Fig. 5B). For example, daily

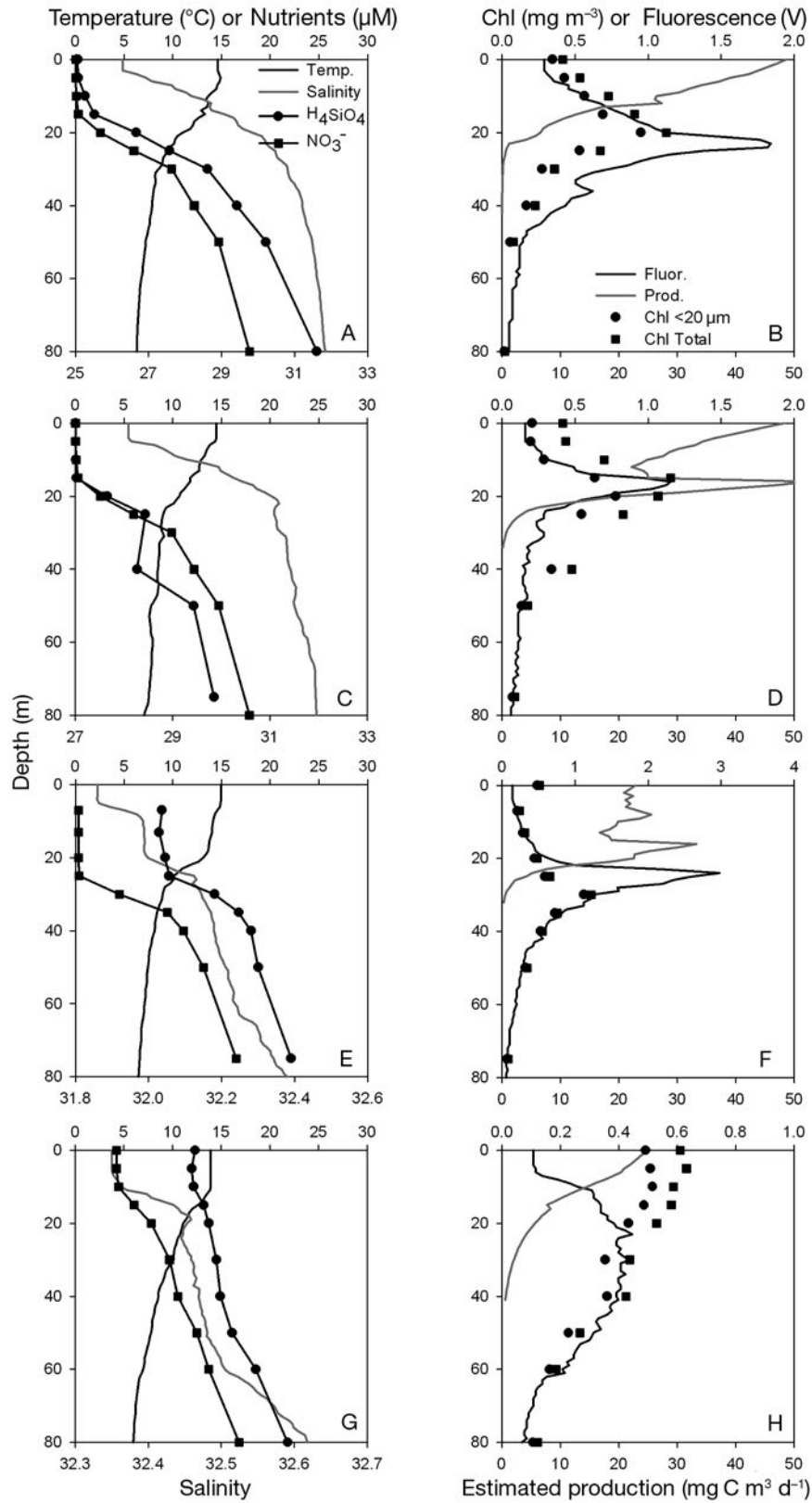


Fig. 3. Left panels: vertical profiles of salinity, temperature, nitrate and silicic acid concentrations. Right panels: *in situ* chl *a* fluorescence, extracted chlorophyll concentration (<20 μm and total) and estimated daily primary production. (A,B) Station PWS-2 (27 July); (C,D) Station ACC-1 (2 August); (E,F) Station GAK-5 (4 August); (G,H) Station GAK-10 (21 July). See Fig. 1 for station locations

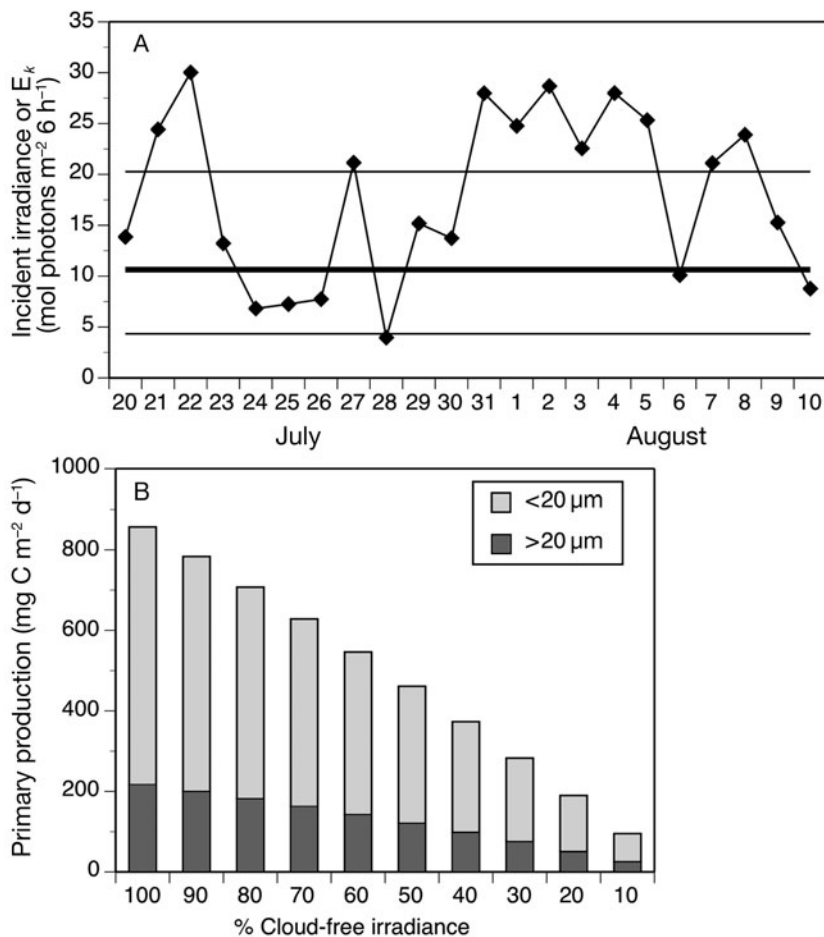


Fig. 4. (A) Incident irradiance during 6 h incubation period (diamonds) in the coastal Gulf of Alaska study region during summer 2003. Natural variation ranged from 15 to 91 % of cloud-free irradiance. Heavy solid line shows average E_k for near-surface phytoplankton; thin lines show minimum and maximum E_k . (B) Modeled effect of cloud cover variability on daily integrated primary production in 2 phytoplankton size fractions in the Alaska Coastal Current

production with the SCM at the shallowest observed depth of 11 m ($927 \text{ mg C m}^{-2} \text{ d}^{-1}$) was roughly twice that with the SCM at the deepest observed depth of 27 m ($453 \text{ mg C m}^{-2} \text{ d}^{-1}$).

DISCUSSION

Photosynthetic parameters

Despite the often heavy cloud cover in the summer CGOA (Fig. 4A), our measured P - E parameters are indicative of a community adapted to high light levels. Hallmarks of low light-adapted communities are high α and, especially, low E_k values (Sakshaug et al. 1997). For example, summer phytoplankton communities in the Ross Sea, Antarctica, had average α and E_k values

of $0.087 \mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons } m^{-2} \text{ s}^{-1}$ and $31 \mu\text{mol photons } m^{-2} \text{ s}^{-1}$, respectively (van Hilst & Smith 2002). In contrast, the average α in our study was $0.014 \mu\text{g C } \mu\text{g chl } a^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons } m^{-2} \text{ s}^{-1}$ (6 times lower) and our average E_k was $390 \mu\text{mol photons } m^{-2} \text{ s}^{-1}$ (12 times higher). In addition, low light-adapted phytoplankton are prone to photoinhibition at high ambient light levels; we saw no photoinhibition even when SCM communities were incubated at sea surface irradiance levels on nearly cloud-free days.

Relatively long P - E incubations such as ours can result in photoacclimation of phytoplankton to incubation conditions (Sakshaug et al. 1997). We did observe positive correlations to incubation irradiance for both P_{\max} and E_k , and weak negative correlations for α (Table 4). However, correlations were approximately as strong (and, in the case of P_{\max} , twice as strong) to the previous day's irradiance (Table 4). Therefore, we believe that measured parameters represent acclimation to environmental light levels, which tended to be coherent over a period of 2 to 3 d (Fig. 4A), and not solely to incubation conditions. It appears that recent light history led to physiological adjustments in summer CGOA phytoplankton, with P_{\max} and E_k responding positively to higher irradiances, and α tending to decrease.

Our measured P - E values closely resemble those from lower-latitude, high-light regions including the southwest Mediterranean Sea (Morán & Estrada 2001), the Southern California Bight (Schofield et al. 1991) and the northern Arabian Sea (Toon et al. 2000). The steep density gradient of the pycnocline effectively creates a shallow bottom in the relatively deep (150 to 200 m) shelf environment, leading to at least intermittent exposure to high irradiances in the surface mixed layer. Low α and high E_k values can also be found in high light-exposed phytoplankton from shallow coastal environments (Kana et al. 1985, Jones 1997 and references therein).

P - E experiments did not reveal major differences between near-surface and SCM phytoplankton communities. P_{\max} and α were indistinguishable. However, E_k showed a tendency to be lower in the SCM, sug-

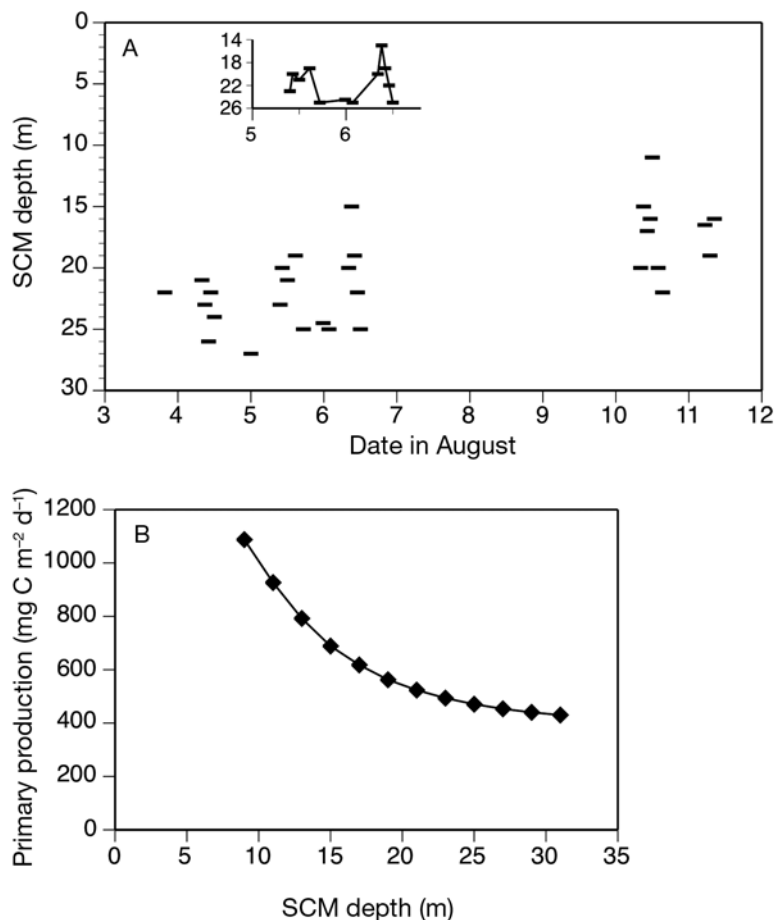


Fig. 5. (A) Depth of subsurface chlorophyll maximum (SCM) at Station GAK-5 during August 2003. Inset shows vertical oscillation of layer during 5 and 6 August, consistent with internal wave activity. (B) Modeled effect of SCM depth on integrated daily water column production

gesting some level of acclimation to the reduced light levels there. Phytoplankton community composition, as indicated by chl *a* size fractionation, also varied somewhat with depth at most stations inshore of GAK-10 (Table 1). Ocean regions with deep euphotic zones and a high degree of physical stability can show strong depth differences in chl-normalized photosynthetic parameters. Consistent changes in P_{\max} and α with depth were observed in the equatorial Pacific Ocean (Lindley et al. 1995) and the western Mediterranean Sea (Morán & Estrada 2001). SCM communities in the Southern California Bight and the offshore waters of the Japan Sea (SCM depth range 25 to 40 m) had consistently lower P_{\max} and E_k values than those near the surface; however, only α differed between the 2 communities in the coastal Japan Sea (Schofield et al. 1991, Yoshikawa & Furuya 2008).

Why were P - E parameters of near surface and SCM phytoplankton so similar during summer 2003? In the summer CGOA, it is likely that the light levels ex-

perienced by near surface and SCM phytoplankton are not consistently different enough to allow development of strongly contrasting P - E responses. There are at least 2 reasons for this. First, the CGOA region has strong tides that are a source of considerable mixing and displacement energy (Henson 2007). Data that we collected on the mid-shelf (Fig. 5A) show that internal wave-like features can cause rapid vertical displacements of the SCM over depth scales (~ 10 m) nearly as large as those separating near surface and SCM communities (see Table 1). Time scales of variation in the vertical distribution of irradiance, due to such displacement events, may be more rapid than time scales of photoacclimation of P_{\max} and α (Lewis et al. 1984). Second, the shallow pycnocline and associated nutricline typical of summer (Fig. 3) give rise to a relatively shallow SCM. The difference in irradiance between near-surface and SCM communities is rivaled by the day-to-day variations in incident irradiance in this environment, which are large (Fig. 4A). An SCM at 21 m (the mid-shelf average for our study period) received about 10% of the irradiance experienced at 3 m (approximately the mid point of the surface mixed layer). Therefore a 21 m SCM on a sunny day received only a little less light than the near-surface community on a day with heavy cloud cover. These several sources

of variability in irradiance probably precluded development of major differences in P_{\max} and α between the 2 communities.

In general, photosynthetic parameters did not vary with location in the coastal Gulf of Alaska during sum-

Table 4. Correlation coefficients for relationships between photosynthetic parameters and incident irradiance (E_0) during the P - E incubation (mol photons $m^{-2} h^{-1}$) or during the previous day (mol photons $m^{-2} d^{-1}$). P - E parameters were estimated for 2 different phytoplankton size classes ($>20 \mu m$ and $<20 \mu m$). * $p < 0.10$, ** $p < 0.05$

	Phytoplankton size	E_k	α	P_{\max}
Incubation E_0	>20	0.53*	-0.12	0.35
	<20	0.60**	-0.42*	0.39
Previous day's E_0	>20	0.44	-0.24	0.53*
	<20	0.52*	-0.12	0.65**

mer 2003. The exceptions were the 2-fold higher P_{\max} and E_k values in the ACC (Fig. 2). Elevated P_{\max} and E_k may be associated with a different phytoplankton species composition in the ACC, which supported a much higher proportion of $>20 \mu\text{m}$ cells than did other regions (Table 1). Microscopic observations showed that *Synechococcus* and prymnesiophytes were common at all stations, cryptophytes were common inshore of slope Station GAK-10, while ACC communities contained, in addition, numerous diatoms and frequently the large dinoflagellate *Ceratium*. *Chaetoceros* was the most frequently observed diatom genus, and *Pseudo-nitzschia* and *Cylindrotheca* were often noted to be present. We have presented evidence (Strom et al. 2006) that iron limitation on the mid- and outer shelf in the Seward Line region plays a role in creating a small cell-dominated community and in restricting growth of diatoms. The current data set also shows the high residual silicic acid concentrations and preponderance of small phytoplankton that would be expected given mid- and outer shelf iron limitation (Fig. 3). Greater iron availability near shore might promote changes in E_k and P_{\max} through direct stimulatory effects on light-harvesting pigments as well as the numerous Fe-containing elements of photosynthetic electron transport (Raven et al. 1999). Relief of iron or nitrogen limitation could also promote changes in photosynthetic parameters through effects on phytoplankton taxonomic composition (Kirk 1994). Although our sampling methods were not trace metal clean, more than 6 h are required for the photophysiology of natural phytoplankton communities to respond to even deliberate iron additions (Behrenfeld et al. 1996, Boyd et al. 1998). Therefore, we consider our parameter estimates to be representative of ambient conditions.

Phytoplankton size class influenced both P_{\max} and α , with values of both parameters averaging $2.5\times$ higher for small ($<20 \mu\text{m}$) phytoplankton than for large ($>20 \mu\text{m}$) phytoplankton (Fig. 2). The discrepancy appears to be related to the differing C:chl a ratios of these size fractions. Combining microscopy-based estimates of phytoplankton C biomass with measured chl a values, E. Lessard (pers. comm.) estimated C:chl a ratios of 25 and 65 for phytoplankton communities dominated by large and small cells, respectively, in the summer 2001 CGOA. Applying these to our P_{\max} and α values to generate C-specific (rather than chl-specific) estimates yields identical values for P_{\max} and α for the 2 size classes of $0.11 \mu\text{g C } \mu\text{g C}^{-1} \text{ h}^{-1}$ and $3.1 \times 10^{-4} \mu\text{g C } \mu\text{g C}^{-1} \text{ h}^{-1}$ per $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, respectively. Assuming these C:chl a ratios are applicable to our data, these 2 size classes were performing identically per unit C biomass; in other words, the large phytoplankton size class required a higher chl a content to achieve the same C-specific photosynthetic perfor-

mance as the small phytoplankton. The higher chl a requirement may arise in part from self-shading of chloroplasts in larger cells (Kirk 1994).

Estimated water column productivity

Summer 2003 productivities in the CGOA were moderate, ranging from 359 to 748 $\text{mg C m}^{-2} \text{ d}^{-1}$ at studied stations, and up to 909 $\text{mg C m}^{-2} \text{ d}^{-1}$ based on indirect estimates (Table 2). Although limited in scope (we had only 4 stations with complete sets of P - E data for both near-surface and SCM communities), these estimates agree well with integrated production values obtained from the region during July and August 2000 to 2004 using 24 h incubations under simulated *in situ* conditions of water samples from multiple depths (D. Stockwell & T. Whitley pers. comm.). On the other hand, our daily production rates were generally higher than those in more strongly stratified areas such as the southeastern Bering Sea. Rho & Whitley (2007) reported values mostly $<500 \text{ mg C m}^{-2} \text{ d}^{-1}$ for July and August during two 4 yr periods of study on the Bering Sea shelf, although occasional productivities exceeding $1000 \text{ mg C m}^{-2} \text{ d}^{-1}$ did occur. Similarly, summer productivities in strongly stratified Prince William Sound typically ranged between ~ 50 and $\sim 500 \text{ mg C m}^{-2} \text{ d}^{-1}$ depending on location, with a few higher values in the ~ 700 to $\sim 1200 \text{ mg C m}^{-2} \text{ d}^{-1}$ range (Goering et al. 1973 as cited in Sambrotto & Lorenzen 1986). In contrast, northeastern Pacific coastal regions with larger nutrient inputs can have several-fold higher summer productivity levels. For example, entrainment of subsurface (ocean-derived) nutrients into the euphotic zone by the Fraser River plume, aided by tidal mixing and short-lived wind events, resulted in August productivities of $>2000 \text{ mg C m}^{-2} \text{ d}^{-1}$ at some Strait of Georgia stations (Yin et al. 1997).

Summer (June to September) productivities at Ocean Station P in the oceanic Gulf of Alaska are strikingly similar to productivities we measured on the shelf. Values obtained during the 1987–1988 SUPER program ranged from 360 to 1540 $\text{mg C m}^{-2} \text{ d}^{-1}$ with an overall mean of 750 $\text{mg C m}^{-2} \text{ d}^{-1}$ ($n = 27$, Welschmeyer et al. 1993). During the 1992 to 1997 cruises of the Canadian Joint Global Ocean Flux Study (JGOFS) program, values ranged from ~ 400 to $\sim 1300 \text{ mg C m}^{-2} \text{ d}^{-1}$, with a mean of 850 $\text{mg C m}^{-2} \text{ d}^{-1}$ ($n = 12$, Boyd & Harrison 1999). Intuitively it is surprising that daily summer production in the low-chl, strongly iron-limited waters of the oceanic Gulf of Alaska should be as high as that on the shelf. Factors contributing to high productivities at Ocean Station P include the deep euphotic zone, the preponderance of small ($<20 \mu\text{m}$) phytoplankton, which, as noted, have high chl-specific

C fixation rates, and the relatively stable nutrient environment, which allows physiological acclimation and community-level adaptation to iron limitation. While shelf phytoplankton appear to experience nutrient input events leading to bursts of summer production (see above), this same variability may preclude physiological acclimation to the generally limiting concentrations of nitrogen and (in some areas) iron, just as variability in day-to-day irradiance appears to preclude photoacclimation to low light.

Effects of environmental variation on primary production

Our data clearly show the major role of light availability in limiting photosynthesis rates and primary production in the summer CGOA. Light limitation derives from at least 3 underlying causes: (1) the high incidence of days with heavy cloud cover; (2) the depth of the pycnocline and associated SCM, which reduces the light available to the majority of the water column phytoplankton biomass; and (3) the photophysiology of the phytoplankton community, which was adapted to high light levels. Each of these factors could be altered by climate-driven changes in the ecosystem. Summers with less cloud cover should result in higher primary production. Somewhat counter-intuitively, summers with more cloud cover, especially if chronic, could also lead to increased production, because a less variable day-to-day light environment might lead to development of a phytoplankton community adapted to low light (i.e. phytoplankton cells able to achieve higher photosynthesis rates at low light levels). SCM depth is another climate-related variable important in determining summer production. Phytoplankton in the SCM sometimes supported close to one half of the total water column productivity during summer 2003 (Table 3) and, because communities were adapted to high light levels, productivities were quite sensitive to the depth of this feature (Fig. 5). The depth of the SCM is set by the pycnocline, which is largely a function of temperature stratification during summer in areas offshore from the ACC (Weingartner et al. 2005). Summer SCM depth was relatively constant during the first 5 yr of the US GLOBEC study period, averaging 18 to 20 m from 1998 through 2002 (Fig. 6). However, during 2003 and 2004 the summer SCM was shallower at 12 to 16 m, demonstrating that substantial year-to-year differences do occur. In general, 2003 was an unusually warm year in the CGOA (Royer & Grosch 2006), and this led to stronger temperature stratification and a shallower pycnocline (Fig. 6).

Because of the high latitude of the CGOA, it has been hypothesized that light limitation is the main

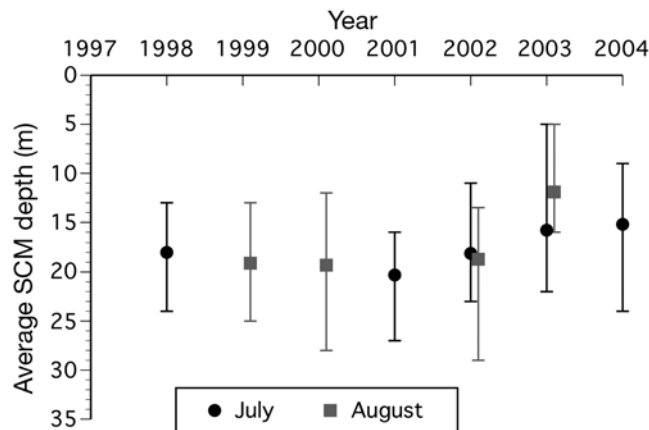


Fig. 6. Variation in depth of subsurface chlorophyll maximum (SCM) on the coastal Gulf of Alaska shelf during summers from 1998 to 2004, from US GLOBEC Long-Term Observation Program (LTOP) data. Values are means of SCM depth at Seward Line shelf stations GAK-1 through GAK-9 (Fig. 1) during July and August; bars show range of observations

environmental variable controlling primary production in that ecosystem. If so, environmental changes that decrease the mixed layer depth (and thus increase light availability to mixed layer phytoplankton) should promote increased production (the 'optimal window of stability', Gargett 1997). While this model is supported by our *P-E* data, it is not supported by the complete picture of production limitation in the CGOA. Inner and mid-shelf phytoplankton demonstrate N-limited growth during the late spring bloom, and this continues throughout the summer stratified period. Indeed, this is an underlying reason for the summer formation of the SCM on the pycnocline and associated nutricline. Further, there is considerable evidence that outer and mid-shelf phytoplankton are chronically iron-limited on portions of the CGOA shelf (Strom et al. 2006). Finally, phytoplankton biomass, an important determinant of primary productivity, is strongly regulated by microzooplankton grazing in the CGOA. Data from spring and summer 2001 showed that all production by $<20 \mu\text{m}$ phytoplankton, and approximately half the production of large ($>20 \mu\text{m}$) phytoplankton, was consumed by microzooplankton in this ecosystem (Strom et al. 2007). Therefore, effects of climate variation on primary production can only be understood through their combined effects on light availability, nutrient supply and microzooplankton biomass and activity levels.

SUMMARY

P-E experiments conducted in summer on the northern CGOA shelf revealed a phytoplankton community

adapted to high levels of light: E_k values were high, photosynthetic efficiencies were low and photoinhibition was never observed. We attribute high light acclimation to the shallow pycnocline and the large short-term variations in irradiance generated by internal waves and variable cloud cover. Small phytoplankton (<20 μm) were responsible for most of the daily summer production, due to their dominance of total chl *a* at most stations and to their higher chl-specific photosynthesis rates. Elevated P_{max} and E_k in the Alaska Coastal Current may have been due to greater iron availability and/or differences in phytoplankton species composition in this near-shore region. Estimated primary productivities in the summer CGOA were moderate, generally exceeding those from more strongly stratified subarctic waters, but less than those in coastal North Pacific regions with greater nutrient supply to summer surface waters. Light limitation of summer primary production in the CGOA arose from both environmental and physiological factors, including (1) the high incidence of days with heavy cloud cover; (2) the depth of the pycnocline and associated SCM, which reduced the light available to the majority of the water column phytoplankton biomass; and (3) high variability in irradiance, which precluded development of a low-light-adapted phytoplankton community. Climate change could thus affect summer photosynthesis rates in the coastal Gulf of Alaska through changes in stratification, wind mixing energy and cloud cover. However, summer phytoplankton growth in this region is also limited by nutrient availability and microzooplankton grazing, indicating a potentially complex relationship between phytoplankton production and environmental variation.

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