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-
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, µmol photons m⁻² s⁻¹), and a Seatech

![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](image)
FL0500 submersible fluorometer for detection of \textit{in situ} chlorophyll \(a\) (chl \(a\)) fluorescence. Incident irradiance \((E_0)\) was measured continuously by a Li-Cor 2\(\pi\) 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 µCi) \(^{14}\)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 ~13:00 h). Experiments were terminated by dividing the contents of each bottle into 2 portions, measuring the volume of each (~150 ml), and then filtering one through a 25 mm polycarbonate filter (0.7 µm nominal pore size) and the other through a 25 mm glass fiber filter (0.7 µm nominal pore size). Filters were placed in 20 ml plastic scintillation bottles into 2 portions, measuring the volume of each (~150 ml), and then filtering one through a 25 mm glass fiber filter (0.7 µm nominal pore size) and the other through a 25 mm polycarbonate filter with 20 µm 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 (µg 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 µm pore size polycarbonate filter over a glass fiber filter (0.7 µm nominal pore size). Samples were extracted in 90% acetone for ~24 h at ~20°C and chl \(a\) concentration determined fluorometrically (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 \((P^a, \mu g\ C\ \mu g\ chl\ a^{-1}\ h^{-1})\) for further analysis.

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

\[
P^a = \tanh \left( \frac{\alpha E}{P_{\text{max}}} \right)
\]

where \(\alpha\) is photosynthetic efficiency and \(P_{\text{max}}\) 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 \(P_{\text{max}}/\alpha.\) \(E_k\) represents the optimal irradiance for photosynthesis (Sakshaug et al. 1997). Curve-fitting and parameter estimation was done separately for <20 and >20 µm 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 In-transformed subsurface PAR profiles. Separate \(k\) values were determined for the surface mixed layer \((k_{\text{surf}})\) and the SCM layer (extending from the top of the SCM to the bottom of the euphotic zone; \(k_{\text{SCM}}\)). Estimation was done iteratively so that only euphotic zone depths (i.e. to 1% \(E_0\)) were included in the calculation of \(k\). Irradiance \((E_0;\ \mu\text{mol}\ \text{photons}\ \text{m}^{-2}\ \text{h}^{-1})\) at each meter depth \((z)\) and for each hour of the day was predicted from \(k\) values and incident irradiance \((E_0)\) according to \(E_z = E_0e^{-k_{\text{surf}}dz}\) for depths above the SCM, and \(E_z = E_{\text{SCM}}e^{-k_{\text{SCM}}dz}\), where \(E_{\text{SCM}}\) 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 \textit{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 \textit{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 µm size class, were used to predict chl\(_{>20}\) and chl\(_{<20}\) at each meter depth from 1 m averaged \textit{in situ} fluorescence profiles collected during morning \(P-E\) casts. No predictive relationship between extracted chl \(a\) and \textit{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:

$$P_{>20} = \text{chl}_{>20} \frac{P_{>20}}{P_{\text{max} >20}} = \text{chl}_{>20} \tanh \left( \frac{\alpha_{>20} E}{P_{\text{max} >20}} \right)$$

where $\text{chl}_{>20}$ is the concentration of chl a (mg m$^{-3}$) in the >20 µm size fraction and $P_{>20}$ is the volume-normalized primary productivity in the >20 µm phytoplankton size fraction (mg C m$^{-3}$ 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 ($P_{\text{INT}}$, mg C m$^{-2}$ 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 $P_{\text{INT}}$ 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 $P_{\text{INT}}$.

### RESULTS

#### Photosynthetic parameters

For experiments in which it could be estimated, $P_{\text{max}}$ ranged from 0.9 to 4.9 µg C µg chl a$^{-1}$ h$^{-1}$ for large (>20 µm) phytoplankton, and from 2.9 to 12.9 µg C µg chl a$^{-1}$ h$^{-1}$ for small (<20 µm) phytoplankton (Table 1). Photosynthesis was never observed. Photosynthetic efficiency ($\alpha$) for large phytoplankton ranged from 0.003 to 0.016 µg C µg chl a$^{-1}$ h$^{-1}$ per µmol photons m$^{-2}$ s$^{-1}$ and for small phytoplankton from 0.012 to 0.033 µg C µg chl a$^{-1}$ h$^{-1}$ per µmol photons m$^{-2}$ s$^{-1}$ (Table 1). $P_{\text{max}}$ and $\alpha$ were uncorrelated. The light saturation parameter ($E_k$) ranged from 190 to 940 µmol photons m$^{-2}$ 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>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>Depth (m)</th>
<th>T (°C)</th>
<th>$E_0$ (mol photons m$^{-2}$)</th>
<th>Chl a (µg l$^{-1}$) frac &gt; 20</th>
<th>$P_{\text{max} &gt;20}$ (µg C µg chl a$^{-1}$ h$^{-1}$)</th>
<th>$P_{\text{max} &lt;20}$ (µg C µg chl a$^{-1}$ h$^{-1}$)</th>
<th>$\alpha$ (µg C µg chl a$^{-1}$ h$^{-1}$ per µmol photons m$^{-2}$ s$^{-1}$)</th>
<th>$E_k$ (µmol photons m$^{-2}$ s$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 Jul</td>
<td>GAK-10</td>
<td>6</td>
<td>13.9</td>
<td>22.3</td>
<td>0.69</td>
<td>0.17</td>
<td>2.26</td>
<td>2.95</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td></td>
<td>17</td>
<td>26.9</td>
<td>0.60</td>
<td>0.15</td>
<td>2.77</td>
<td>4.58</td>
<td>0.008</td>
<td>0.019</td>
</tr>
<tr>
<td>23 Jul</td>
<td>GAK-10</td>
<td>9</td>
<td>13.9</td>
<td>12.4</td>
<td>0.54</td>
<td>0.19</td>
<td>nd</td>
<td>nd</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>18</td>
<td>13.3</td>
<td>0.62</td>
<td>0.18</td>
<td>3.03</td>
<td>5.37</td>
<td>0.010</td>
<td>0.020</td>
</tr>
<tr>
<td>25 Jul</td>
<td>PWS-2</td>
<td>4.5</td>
<td>14.7</td>
<td>6.2</td>
<td>0.43</td>
<td>0.44</td>
<td>nd</td>
<td>nd</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>21</td>
<td>7.3</td>
<td>1.41</td>
<td>0.18</td>
<td>nd</td>
<td>nd</td>
<td>0.007</td>
<td>0.024</td>
</tr>
<tr>
<td>27 Jul</td>
<td>PWS-2</td>
<td>5</td>
<td>14.7</td>
<td>15.0</td>
<td>0.45</td>
<td>0.17</td>
<td>2.05</td>
<td>6.85</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>21</td>
<td>19.1</td>
<td>1.25</td>
<td>0.15</td>
<td>1.36</td>
<td>3.75</td>
<td>0.005</td>
<td>0.019</td>
</tr>
<tr>
<td>29 Jul</td>
<td>ACC-1a</td>
<td>4</td>
<td>14.2</td>
<td>16.5</td>
<td>0.75</td>
<td>0.52</td>
<td>nd</td>
<td>nd</td>
<td>0.010</td>
</tr>
<tr>
<td></td>
<td></td>
<td>19</td>
<td>16.6</td>
<td>1.05</td>
<td>0.39</td>
<td>nd</td>
<td>nd</td>
<td>0.016</td>
<td>0.019</td>
</tr>
<tr>
<td>1 Aug</td>
<td>GAK-1ia</td>
<td>5</td>
<td>14.2</td>
<td>29.2</td>
<td>0.49</td>
<td>0.54</td>
<td>4.14</td>
<td>10.59</td>
<td>0.008</td>
</tr>
<tr>
<td>2 Aug</td>
<td>ACC-1a</td>
<td>4</td>
<td>14.3</td>
<td>29.1</td>
<td>0.39</td>
<td>0.49</td>
<td>4.93</td>
<td>11.43</td>
<td>0.006</td>
</tr>
<tr>
<td></td>
<td></td>
<td>18</td>
<td>27.0</td>
<td>2.36</td>
<td>0.71</td>
<td>3.88</td>
<td>12.89</td>
<td>0.007</td>
<td>0.023</td>
</tr>
<tr>
<td>4 Aug</td>
<td>GAK-5</td>
<td>5</td>
<td>14.6</td>
<td>24.8</td>
<td>0.30</td>
<td>0.13</td>
<td>3.06</td>
<td>6.78</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td></td>
<td>23</td>
<td>28.1</td>
<td>1.55</td>
<td>0.09</td>
<td>0.90</td>
<td>7.01</td>
<td>0.003</td>
<td>0.021</td>
</tr>
<tr>
<td>6 Aug</td>
<td>GAK-5</td>
<td>5</td>
<td>14.6</td>
<td>9.8</td>
<td>0.39</td>
<td>0.10</td>
<td>nd</td>
<td>nd</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15</td>
<td>10.7</td>
<td>1.58</td>
<td>0.08</td>
<td>1.92</td>
<td>8.77</td>
<td>0.007</td>
<td>0.033</td>
</tr>
<tr>
<td>9 Aug</td>
<td>CCSE-3a</td>
<td>4</td>
<td>15.0</td>
<td>16.4</td>
<td>0.68</td>
<td>0.48</td>
<td>nd</td>
<td>nd</td>
<td>0.011</td>
</tr>
<tr>
<td>10 Aug</td>
<td>GAK-5</td>
<td>5</td>
<td>14.6</td>
<td>7.8</td>
<td>0.30</td>
<td>0.13</td>
<td>nd</td>
<td>nd</td>
<td>0.009</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15</td>
<td>9.5</td>
<td>1.29</td>
<td>0.05</td>
<td>3.68</td>
<td>0.004</td>
<td>0.019</td>
<td>200</td>
</tr>
</tbody>
</table>

*Considered Alaska Coastal Current (ACC) station
depths in either $P_{\text{max}}$ or $\alpha$, for either large or small phytoplankton (paired $t$-test, all $p$-values > 0.18). Therefore, $P_{\text{max}}$ and $\alpha$ 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 $P_{\text{max}}$ and $\alpha$ 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 $P_{\text{max}}$ values than large phytoplankton (average 7.1 vs. 2.8 µg C µg chl $a^{-1}$ h$^{-1}$, $p < 0.001$), as well as significantly higher photosynthetic efficiencies (average 0.020 vs. 0.008 µg C µg chl $a^{-1}$ h$^{-1}$ per µmol photons m$^{-2}$ s$^{-1}$, $p < 0.001$). In contrast, phytoplankton size did not affect $E_k$ ($p = 0.585$) (Fig 2C). Location influenced $P_{\text{max}}$ and $E_k$ ($p \leq 0.001$), but not $\alpha$ ($p = 0.578$). Phytoplankton in the Alaska Coastal Current (ACC) had $P_{\text{max}}$ 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 mg C m$^{-2}$ d$^{-1}$ at slope station GAK-10 to 748 mg C m$^{-2}$ 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-11i and HE-2 (Fig. 1). Although integrated chl $a$ concentrations were similar at the 2 stations, HE-2 yielded a higher daily production estimate (909 vs. 617 mg C m$^{-2}$ d$^{-1}$, Table 2).

Small (<20 µm) 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-
shown, as well as their percent contribution to the Gulf of Alaska. Depth-integrated values for each layer are chlorophyll maximum (SCM) layers at 3 stations in the coastal
irradiance (mol photons m \(^{-2}\)); mixed layer/subsurface chlorophyll maximum layer; Z\(_{eu}\): euphotic zone
depth (m); Int chl \(a\) (mg m \(^{-3}\); Int PP (mg C m \(^{-2}\) d \(^{-1}\))

**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). \(E_d\): daily incident irradiance (mol photons m \(^{-2}\)); \(k\): attenuation coefficients (m \(^{-1}\)) for the surface mixed layer/subsurface chlorophyll maximum layer; \(Z_{eu}\): euphotic zone**

<table>
<thead>
<tr>
<th>Date</th>
<th>Station</th>
<th>(E_d)</th>
<th>(k)</th>
<th>(Z_{eu})</th>
<th>Chl (a)</th>
<th>PP</th>
<th>Int [% &gt; 20]</th>
<th>Int [% &gt; 20]</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direct</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>21 Jul</td>
<td>GAK-10</td>
<td>37.9</td>
<td>0.15</td>
<td>0.09</td>
<td>41</td>
<td>24.8</td>
<td>17</td>
<td>359</td>
</tr>
<tr>
<td>27 Jul</td>
<td>PWS-2</td>
<td>32.8</td>
<td>0.14</td>
<td>0.09</td>
<td>42</td>
<td>26.6</td>
<td>21</td>
<td>581</td>
</tr>
<tr>
<td>2 Aug</td>
<td>ACC-1</td>
<td>49.3</td>
<td>0.12</td>
<td>0.15</td>
<td>34</td>
<td>35.3</td>
<td>38</td>
<td>748</td>
</tr>
<tr>
<td>4 Aug</td>
<td>GAK-5</td>
<td>50.7</td>
<td>0.14</td>
<td>0.15</td>
<td>32</td>
<td>34.5</td>
<td>9</td>
<td>524</td>
</tr>
<tr>
<td>Indirect</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 Aug</td>
<td>GAK-1i</td>
<td>43.2</td>
<td>0.11</td>
<td>0.11</td>
<td>41</td>
<td>38.6</td>
<td>45</td>
<td>617</td>
</tr>
<tr>
<td>8 Aug</td>
<td>HE-2</td>
<td>37.4</td>
<td>0.07</td>
<td>0.19</td>
<td>24</td>
<td>36.2</td>
<td>77</td>
<td>909</td>
</tr>
</tbody>
</table>

**Table 3. Partitioning of daily primary production (PP, mg C m \(^{-2}\) d \(^{-1}\)) and chl \(a\) (mg chl \(a\) m \(^{-3}\)) 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)**

<table>
<thead>
<tr>
<th>Station Date (2003)</th>
<th>Layer</th>
<th>Depth range (m)</th>
<th>PP % total</th>
<th>Chl (a) % total</th>
</tr>
</thead>
<tbody>
<tr>
<td>PWS-2 27 Jul</td>
<td>Surface</td>
<td>0–11</td>
<td>453</td>
<td>78</td>
</tr>
<tr>
<td>ACC-1 2 Aug</td>
<td>Surface</td>
<td>0–12</td>
<td>437</td>
<td>58</td>
</tr>
<tr>
<td>GAK-5 4 Aug</td>
<td>Surface</td>
<td>0–13</td>
<td>299</td>
<td>40</td>
</tr>
</tbody>
</table>

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 \(E_d\) values with midday irradiance levels taken over a 6 h period showed that, based on the study-wide average \(E_d\) of 10.6 mol photons m \(^{-2}\) 6 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 mol photons m \(^{-2}\) d \(^{-1}\) (15 to 91 % of the maximum cloud-free irradiance of 56 mol photons m \(^{-2}\) 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.
production with the SCM at the shallowest observed depth of 11 m (927 mg C m\(^{-2}\) d\(^{-1}\)) was roughly twice that with the SCM at the deepest observed depth of 27 m (453 mg C m\(^{-2}\) 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 \(\alpha\) and, especially, low \(E_k\) values (Sakshaug et al. 1997). For example, summer phytoplankton communities in the Ross Sea, Antarctica, had average \(\alpha\) and \(E_k\) values of 0.087 µg C µg chl \(a^{-1}\) h\(^{-1}\) per µmol photons m\(^{-2}\) s\(^{-1}\) and 31 µmol photons m\(^{-2}\) s\(^{-1}\), respectively (van Hilst & Smith 2002). In contrast, the average \(\alpha\) in our study was 0.014 µg C µg chl \(a^{-1}\) h\(^{-1}\) per µmol photons m\(^{-2}\) s\(^{-1}\) (6 times lower) and our average \(E_k\) was 390 µmol photons m\(^{-2}\) 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 \(P_{\text{max}}\) and \(E_k\), and weak negative correlations for \(\alpha\) (Table 4). However, correlations were approximately as strong (and, in the case of \(P_{\text{max}}\), 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 \(P_{\text{max}}\) and \(E_k\) responding positively to higher irradiances, and \(\alpha\) 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 \(\alpha\) 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. \(P_{\text{max}}\) and \(\alpha\) were indistinguishable. However, \(E_k\) showed a tendency to be lower in the SCM, sug-
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 $P_{\text{max}}$ and $\alpha$ 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 $P_{\text{max}}$ and $E_k$ values than those near the surface; however, only $\alpha$ 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 experienced 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 $P_{\text{max}}$ and $\alpha$ (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 $P_{\text{max}}$ and $\alpha$ between the 2 communities.

In general, photosynthetic parameters did not vary with location in the coastal Gulf of Alaska during summer 2003.
mer 2003. The exceptions were the 2-fold higher $P_{\text{max}}$ and $E_k$ values in the ACC (Fig. 2). Elevated $P_{\text{max}}$ and $E_k$ may be associated with a different phytoplankton species composition in the ACC, which supported a much higher proportion of >20 µm 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 $P_{\text{max}}$ 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 $P_{\text{max}}$ and $\alpha$, with values of both parameters averaging 2.5× higher for small (<20 µm) phytoplankton than for large (>20 µm) 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 $P_{\text{max}}$ and $\alpha$ values to generate C-specific (rather than chl-specific) estimates yields identical values for $P_{\text{max}}$ and $\alpha$ for the 2 size classes of 0.11 µg C µg C$^{-1}$ h$^{-1}$ and 3.1 × 10$^{-4}$ µg C µg C$^{-1}$ h$^{-1}$ per µmol photons m$^{-2}$ 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 performance 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 mg C m$^{-2}$ d$^{-1}$ at studied stations, and up to 909 mg C m$^{-2}$ 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. Whitledge 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 & Whitledge (2007) reported values mostly <500 mg C m$^{-2}$ d$^{-1}$ for July and August during two 4 yr periods of study on the Bering Sea shelf, although occasional productivities exceeding 1000 mg C m$^{-2}$ d$^{-1}$ did occur. Similarly, summer productivities in strongly stratified Prince William Sound typically ranged between ~50 and ~500 mg C m$^{-2}$ d$^{-1}$ depending on location, with a few higher values in the ~700 to ~1200 mg C m$^{-2}$ 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 mg C m$^{-2}$ 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 mg C m$^{-2}$ d$^{-1}$ with an overall mean of 750 mg C m$^{-2}$ 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 ~1300 mg C m$^{-2}$ d$^{-1}$, with a mean of 850 mg C m$^{-2}$ 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 µm) 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 5yr 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 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 µm phytoplankton, and approximately half the production of large (>20 µm) 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: $E_\text{a}$ 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 ($<20 \mu m$) 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 $P_{\text{max}}$ and $E_\text{a}$ 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.

Acknowledgements. We thank F. Perez and J. Swanko for help with on-board sampling and chlorophyll analysis, and C. Mordy for nutrient analyses. T. Weingartner provided CTD data processing from our cruise and, with T. Royer, led the LTOP CTD sampling effort that provided data in Fig. 6. K. Bright prepared Fig. 1. J. Napp as chief scientist and the captain and crew of the RV ‘Alpha Helix’ greatly assisted our sampling efforts. This research was funded by National Science Foundation grants OCE-0101397 and OCE-0639093. This is US GLOBEC contribution no. 656.

LITERATURE CITED

of the Northern Gulf of Alaska. Cont Shelf Res 24: 859–897


Editorial responsibility: Matthias Seaman,
Oldendorf/Luhe, Germany

Submitted: November 17, 2008; Accepted: December 11, 2009
Proofs received from author(s): February 22, 2010