

Temporal and spatial variability of photosynthetic parameters and community respiration in Long Island Sound

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ABSTRACT: Photosynthetic parameters and community respiration were measured throughout 3 seasons at 8 stations in central and western Long Island Sound during 2002 and 2003. Light-dark bottle oxygen change was measured in a photosynthesis–irradiance (P – I) series for water from the mixed layer, and respiration was measured for surface, pycnocline, and near bottom water. P – I curves were fitted numerically to calculate biomass-specific rates of maximum photosynthesis at light saturation (P_m^B), photosynthetic efficiency at low irradiance (α^B) and plankton community respiration (R_c). The temporal and spatial variability of these fitted parameters, the derived parameter I_k , and the concentration of phytoplankton pigments were described in relation to each other and to environmental factors. Concentrations of chlorophyll (chl) and phaeopigments (phaeo), and R_c reached maxima in summer and significantly decreased seaward along the length of the Sound. Photosynthetic parameters also reached maxima in summer, however there was no significant spatial variability. In surface waters, the average (\pm SD) of P_m^B (1.3 ± 0.4 mmol O₂ [mg chl]⁻¹ h⁻¹) demonstrated the lowest variability, compared to chl (6.9 ± 4.9 mg m⁻³), phaeo (3.5 ± 2.5 mg m⁻³), α^B (10.9 ± 5.4 μ mol O₂ [mg chl]⁻¹ h⁻¹ [μ E m⁻² s⁻¹]⁻¹), I_k (132.6 ± 71.9 μ E m⁻² s⁻¹), and R_c (1.4 ± 0.9 mmol O₂ m⁻³ h⁻¹). Chl and P_m^B both varied with total daily insolation and with average irradiance of the photic zone, while P_m^B was also correlated with temperature. Although P_m^B and chl increased during summer, their peaks did not occur simultaneously. Temporal trends in α^B were less clear-cut than for P_m^B and chl, but α^B was correlated with light properties of the water column. Plankton community respiration was high in surface waters and decreased with depth. Based on the relationship between R_c and chl, algal-related rates of respiration (R_a) were estimated at ~50% of total plankton community respiration. Our results do not support the common method of estimating algal respiration based on P_m^B .

KEY WORDS: Productivity · Primary production · Respiration · Oxygen · Chlorophyll · Phytoplankton community · Long Island Sound

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INTRODUCTION

Autochthonous phytoplankton production has been targeted as the key contributor to hypoxia in eutrophic systems such as Long Island Sound (LIS), yet has not been well characterized in this system. Although limited investigations of the mechanisms that control hypoxia in LIS have recognized this underlying ecological process (Welsh & Eller 1991, Anderson & Taylor 2001), the scope of such studies did not allow for the characterization of rates in space and time, the estima-

tion of integrated rates for the whole Sound, or formulation of a model of primary production in LIS. As a first step for such calculations, this study reports measurements of temporal and spatial patterns in the photosynthetic characteristics and phytoplankton biomass in relation to each other and to environmental factors.

Photosynthetic parameters are derived from measured variations in the phytoplankton response to light (a photosynthesis–irradiance relationship, or P – I curve; see e.g. Fig. 4). Typically, a linear response at low light levels approaches an asymptotic maximum rate at high

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light levels (Platt & Jassby 1976, Sakshaug et al. 1997), and high-light inhibition may or may not be observed. At least 2 photosynthetic parameters characterize the P - I response: α , the initial slope of the light curve that characterizes photosynthetic efficiency at low irradiance, and P_m , the plateau of the maximum photosynthetic rate at light saturation (Platt & Sathyedranath 1993). In some instances, a third parameter β is necessary to describe photoinhibition, the reduction in productivity at higher irradiance levels (Platt et al. 1980). The version of the equation used by Walsby (1997) includes plankton community respiration (R_c). This formulation is applicable only to oxygen determinations, since the ^{14}C method does not allow estimates of respiration (Platt & Jassby 1976, Cote & Platt 1983, Bender et al. 1987). Expressing these parameters in biomass-specific form, i.e. α^B and P_m^B , removes the effect of standing stock so that these physiological parameters are independent of changes in biomass. The derived parameter $I_k (= P_m^B/\alpha^B)$ evaluates where the initial slope intersects the maximum, providing a useful measure of the light level at which photosynthesis is saturated (Figueiras et al. 1994).

Variation in the calculated biomass-specific photosynthetic parameters is used to characterize functional changes in the phytoplankton community, including physiological acclimation and shifts in community structure. Such variations provide quantitative insight into the effects of varying environmental conditions on specific phytoplankton production rates that are unresolved with the use of the measured volume-specific rates (Cote & Platt 1983, 1984). Characterizing P - I parameters in LIS enables synoptic estimates of the temporal and spatial variability in phytoplankton production for the first time (Goebel et al. 2006).

In this paper, we characterize the temporal and spatial variability of physiological parameters of the P - I response (α^B , P_m^B and R_c) from direct measurements of oxygen change in samples collected from central and western Long Island Sound (cwLIS) over 3 seasons during 2002 and 2003. We explore the relationships among phytoplankton metabolic rates and biomass, as well as their relationships to observed physical and chemical environmental parameters. Furthermore, we test the relationships between R_c and phytoplankton biomass or P_m^B , to estimate an algal-related rate of respiration in LIS.

MATERIALS AND METHODS

Site description. Long Island Sound, typically divided into western, central and eastern segments, is 160 km long and 5 to 32 km wide, with a mean depth of 21 m and a bottom depth of 30 to 60 m throughout the central and

western basins. The tide is predominantly semidiurnal (Wong 1990), with an average tidal amplitude that increases 4-fold (0.7 to 2.1 m) from the eastern to the western end of the Sound (<http://co-ops.nos.noaa.gov/tides05/tab2ec2a.html#16>). The turnover time for the entire Sound is 63 to 166 d (Turekian et al. 1996). Adjacent watersheds are highly populated, with more than 8 million people within the LIS drainage basin. In particular, the western end of LIS receives a large input of sewage from New York City and densely populated SW Connecticut. Salinity stratification begins during the inflow of freshwater from winter snow melt and spring rains. During the summer, physical stratification of the water column in central and western LIS (cwLIS) increases with increasing insolation and heating of surface waters (Welsh & Eller 1991, Anderson & Taylor 2001). Increased thermal stratification and relatively weak tidal and wind mixing inhibit ventilation of bottom water, leading to deteriorating oxygen levels (Welsh & Eller 1991, Torgersen et al. 1997). Stratification and increasingly hypoxic conditions are usually disrupted by storms during autumn, and occasionally during summer (Anderson & Taylor 2001).

Cruise plan. We sampled 8 stations spanning cwLIS during 15 surveys of 2 to 3 d; 6 stations were uniformly distributed along the main axis of cwLIS (Stns A4, C1/C2, D3, E1, F2/F3, H4) and 2 stations were transversely distributed (Stns 9, 15) (Fig. 1). Survey cruises were biweekly during the summers of 2002 and 2003 and monthly during autumn 2002, and late spring and autumn 2003.

Sampling regime. At each station, a Seabird SBE-19 SeaCat Profiler equipped with a YSI Model 5739 O_2 sensor, a spherical Licor PAR (photosynthetically active radiation) sensor, underwater model 193SA, and a WET Labs WETStar fluorometer was used to vertically profile salinity, temperature, dissolved oxygen, irradiance and chlorophyll fluorescence. The profiler was mounted on a General Oceanics Model 1015 rosette system that was also used to collect water at the surface (1 to 2 m), mid-depth (within the pycnocline), and near bottom (1 to 2 m from the bottom). Discrete samples were filtered and analyzed for pigments; particulate C and N were also determined but are not reported here. Fluorometer and dissolved oxygen CTD data were calibrated with *in situ* water samples; these profile data were supplied by the State of Connecticut Department of Environmental Protection (CTDEP).

Underwater irradiance. Attenuation coefficients (K ; m^{-1}) were calculated as the slope of the natural log of irradiance with depth (Kirk 1994). The depth of the photic zone (Z_p) was defined as 1% of subsurface (0.2 m) irradiance, so that $Z_p = 4.6/K$. Average irradiance within the photic zone (\bar{I}_{Z_p}) was calculated using the following equation (Kremer & Nixon 1978):

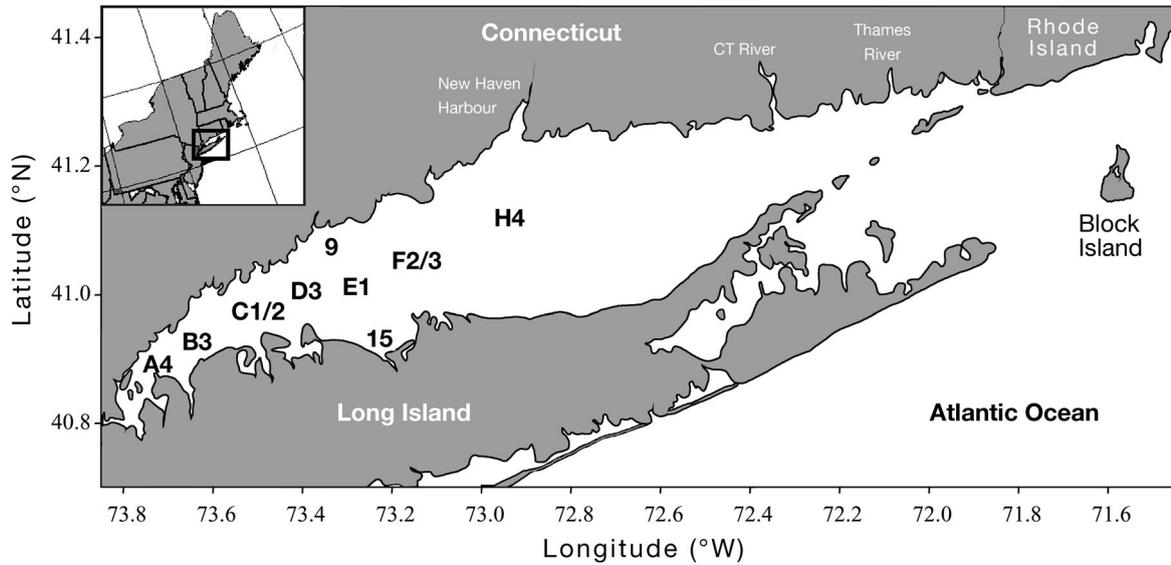


Fig. 1. Long Island Sound (LIS) and stations sampled. Inset: location of LIS on the NE coast of continental USA

$$\bar{I}_{Z_p} = I_0 (1 - e^{-K Z_p}) / (K Z_p) \quad (1)$$

where I_0 is average daytime instantaneous incident irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$). An analogous calculation was used for average irradiance in the mixed layer ($\bar{I}_{Z_{ml}}$) by replacing Z_p with Z_{ml} in Eq. (1). Depth of the mixed layer (Z_{ml}) was determined using density profiles from the CTD casts, and defined as the depth at which density (σ_t) remains similar to that at the surface. Profiles of temperature, salinity and fluorescence from CTD casts were used to corroborate Z_{ml} when σ_t was ambiguous. When stratification was not distinct, the criterion used to distinguish a stratified from a well-mixed water column was a density difference (σ_t) between bottom (maximum) and surface (minimum) waters $< 0.5 \text{ kg m}^{-3}$ (Anderson & Taylor 2001). In cases of a mixed water column ($\sigma_t < 0.5 \text{ kg m}^{-3}$), Z_{ml} equaled the entire depth of the water column.

Chlorophyll analysis. Triplicate samples of 250 ml from each sampled depth were filtered in the field for chlorophyll (chl) concentration through GF/F filters, transported to the laboratory on ice, and frozen until analyzed (within 2 d). Filters were extracted in 7 ml of 90% acetone overnight (18 to 20 h), mixed well, centrifuged, and read at room temperature fluorometrically before and after acidification with 2 drops of 10% HCl. The Turner Designs Model TD-700 fluorometer was calibrated with pure chl *a* (semiannually) and a supplied solid standard (daily). Chl and phaeopigment (phaeo) concentrations were calculated with published equations (Parsons et al. 1984).

Productivity measurements. The $P-I$ parameters were determined for rates of change of dissolved oxy-

gen (O_2) in light and dark bottles. The oxygen method provides several advantages over the more commonly used ^{14}C method in productive coastal waters. Unlike ^{14}C , which appears to measure something between gross and net primary production (Bender et al. 1987), measurement of the changes in O_2 enables the discrimination between net and gross production. This was also tested in the present study, in a comparison of $P-I$ curves derived from O_2 and ^{14}C methods. Although the yield of biomass under nutrient-depleted conditions may not be represented by O_2 -based production, we do not consider this to be an issue in the nutrient replete waters of LIS. The O_2 method also enables reliable measurements of plankton community respiration, a rate unattainable with ^{14}C . Furthermore, O_2 is of fundamental interest in the study of LIS hypoxia, and direct measurements in this currency make sense.

Metabolic rates were determined in 300 ml borosilicate (Pyrex) BOD bottles. Bottles were filled with an unfiltered, homogenous sample of surface water from the upper mixed layer. Each $P-I$ series consisted of 12 light, 3 dark and 3 initial bottles. Triplicate dark-incubated bottles and initial O_2 concentrations were also measured on unfiltered samples from mid- and near-bottom depths. The BOD bottles were filled by overflowing with at least half a bottle volume, to avoid bubbles and air contamination. Bottles were stoppered before being placed in temperature-controlled incubators for 2 to 4 h. Dark bottles were incubated in either an incubator cooled with surface water (observed temperature range was 2.5 to 25.6°C) or an insulated box containing water from depths sampled (for pycnocline and bottom samples, the observed temperature range was 1.8 to 24.0°C). Incubation tem-

peratures were maintained within 2 to 3°C of *in situ* temperatures. Light bottles were placed in a flow-through incubator cooled with surface water and illuminated with an Osram Sylvania Metalarc® (metal halide) lamp. Bottles were exposed to a light gradient encompassing the irradiance range of the photic zone in LIS, from ~30 to 1500 $\mu\text{E m}^{-2} \text{s}^{-1}$. Light levels were achieved by different distances from the light source, in some cases modulated with mesh screening. Light levels were measured at the midpoint of a seawater-filled BOD bottle at each position of the incubator with a spherical PAR sensor Biospherical Instruments underwater model QSP-2100 (3.7 pi collector). Initial and incubated BOD bottles were fixed with chemical reagents for the Winkler method (manganous sulfate and alkaline iodide; Parsons et al. 1984), stoppered, sealed with water around the neck, and capped, in order to avoid contamination of samples from evaporation and air exchange around the stopper, and returned to the laboratory for subsequent analysis (within 1 wk).

O₂ analysis. Winkler titrations were carried out in the UCONN laboratory with a computer-controlled automatic titrator (Friederich 1991). This automated titrator analyzes the sample with a photometric detector to determine the endpoint at the wavelength of peak absorbance of the yellow iodide complex. Samples are titrated beyond the endpoint; the endpoint is determined as the intersection of linear regressions prior to and after the absorbance ceases to change with thiosulfate addition. A computer-controlled Kloehe digital pipette pump delivers increments down to 0.0005 ml thiosulfate, a precision of 0.03 mmol O₂ m⁻³. Replicate titrations with standards have a standard deviation of 0.06 mmol O₂ m⁻³ (n = 5), far better than natural variability in our replicate field samples (standard deviation of ~1 mmol O₂ m⁻³).

P–I curve-fitting procedure. Changes in net oxygen production of the plankton community (NCP) and consumption (R_c) in surface waters were normalized by average chl stock and plotted as a function of irradiance. Various equations have been used to model P–I data, resulting in substantial testing and discussion of their relative merits (Platt & Jassby 1976, Aalderink & Jovin 1997, Gilbert et al. 2000). Aalderink & Jovin (1997) and Gilbert et al. (2000) tested the variability of different model fits. Aalderink & Jovin (1997) demonstrated that the 8 models they compared could not be distinguished by their goodness of fit at the 90% level of confidence. Gilbert et al. (2000) also found that no model was superior, emphasizing that comparison of data sets should use the same model. We initially evaluated 4 models for calculated net photosynthetic rate of the community (P_c): (Webb et al. 1974, Jassby & Platt 1976, Platt et al. 1980, Walsby 1997). The following

model was chosen from Platt et al. (1980), as modified by Walsby (1997), to include photoinhibition.

$$P_c = P_m^B \left[1 - \exp\left(-\alpha^B \frac{I}{P_m^B}\right) \right] - R_c^B + (\beta I) \quad (2)$$

This model fit our data well and was also used by Walsby (1997) for rates of production using oxygen evolution including a chlorophyll-normalized parameter for oxygen consumption (R_c^B). The interpretation of R_c^B is questionable, so the more meaningful R_c was fitted to Eq. (2) utilizing non-chlorophyll-specific (i.e. volumetric) oxygen change data (i.e. α and P_m).

The non-linear Levenberg-Marquardt curve-fitting algorithm (FIT) and confidence interval (CONFINT) functions in Matlab® were used to fit the P–I model to our data yielding estimates with 95% confidence intervals for biomass-specific P–I parameters (α^B and P_m^B) and community respiration (R_c). This curve fitting procedure requires initial estimates, but no specific constraints, for the adjusted parameters. Photoinhibition was not observed and β was set equal to zero. With no necessary correction for β , the fitted P_m^B represents the maximum realized instantaneous gross community production (Platt et al. 1980). Selection of P–I curves was based on goodness of fit. The criterion of adjusted $r^2 > 70\%$ resulted in the removal of 10% of the P–I curves. An average coefficient of variation was calculated for the fit of each parameter to the model (Eq. 2). Comparison of R_c measured directly as the average of 3 dark incubations and R_c modeled with the P–I curve fitting procedure demonstrated good agreement ($r^2 = 0.97$, $p < 0.0001$, $n = 98$), well within the standard errors of replicate BOD bottle measurements and P–I curve fits; here modeled values are used.

Spectral quality. To quantify potential effects of the spectral quality of the artificial light incubator, results from the on-deck system were compared to simultaneous incubations run *in situ* at a central station (C1/C2 in Fig. 1). Trials on 2 dates indicated no significant differences between the calculated P–I parameters fitted on the P–I data from samples incubated on-deck versus *in situ*. In the first trial, α^B and P_m^B values and their calculated standard deviations from the fitted P–I curves of the *in situ* and incubated arrays were not significantly different, falling well within the range of variability observed throughout the remainder of this study. Although the parameters were also not significantly different in the second experiment, large variability in the slopes of each curve made it difficult to determine whether α^B was actually not significantly different between the 2 methods. Despite the inconclusive comparison of α^B in Trial 2, there were no significant effects of spectral quality on our *in situ* incubations based on our measurements of P_m^B in both trials, and α^B in the first trial.

Diurnal variability. Since incubations from different stations were initiated at varying times throughout the day, there was a potential bias due to diurnal variations in $P-I$ parameters (Harding et al. 1981, 1982). Possible diurnal effects were investigated in our $P-I$ measurements on 2 occasions during the summer of 2002. A bulk water sample (~20 l) was collected in the morning (~08:00 h), and held in large (20 l) polycarbonate bottles under subdued light for the remainder of the day. We sampled 3 overlapping $P-I$ series and chlorophyll standing stock measurements from this reference sample throughout the daily survey (09:00 to 17:00 h).

No trends in diurnal variability were observed over 2 trial experiments. One of the experiments demonstrated no significant differences among fitted $P-I$ parameters throughout the period of the day. In the other experiment, significant differences occurred, with a minimum α^B in the morning, a minimum P_m^B mid-day, and a maximum P_m^B in the late afternoon. These results were inconclusive and no obvious correction seems justified. In any case, seasonal, spatial and overall averages for $P-I$ parameters were measured at a variety of initial sampling times during the photoperiod with no systematic bias. Therefore any daytime variations in productivity, which might vary with likely but uninvestigated species composition and/or environmental conditions (Harding et al. 1981), are included in the seasonal and annual variability we report.

Statistics. Descriptive statistics (mean, standard deviation, coefficient of variation, range, median, quartiles and range factor (= maximum/minimum)) were calculated for $P-I$ parameters, R_c , chl, phaeo, and irradiance variables measured in this study (see Tables 1 & 2). Statistical descriptors of $P-I$ parameters and respiration exclude outliers (>3 interquartile ranges from the edge of the interquartile range; SPSS v12.0.1). These outliers for fitted parameters are indicated in box plots that display temporal variability (see Figs. 2 & 5), but omitted from plots displaying spatial variability (see Figs. 3 & 6) and from all statistical tests. Survey-wide averages of variables in the text are reported \pm SD, while fitted parameters of linear and non-linear models are reported \pm SE of the estimate.

ANOVA comparisons of the natural log transformations of physiological parameters (α^B , P_m^B , R_c , and I_k), chl and phaeo, and irradiance variables (K or Z_p , Z_{ml} , \bar{I}_{Z_p} , and $\bar{I}_{Z_{ml}}$) were used to test for significant differences, indicated by p-values, in time (month and year) and space (station) (see Table 3). Although natural log transformations improved the normality of the data, Levene's statistical test was significant across all ANOVAs, indicating heterogeneous variances. However, van Belle (2002) states that the Levene's statistic is very sensitive to departures from the assumption of

homoscedasticity and should not prohibit further hypothesis testing. Therefore we proceeded with the multi-way ANOVA. In instances where there were no significant interactions within the 3-way ANOVA, we checked for significant differences among non-homoscedastic variables using 1-way ANOVA and the Welch and Brown-Forsyth robust tests of equality of means (SPSS v12.0.1). This secondary check reversed the significance for monthly variability in light attenuation properties (K or Z_p , and Z_{ml}) only (see Table 3).

With uncertainties in both variables, we applied a weighted Model II linear least squares regression, following Press et al. (1992), to estimate the average relationship between R_c and chl. Log-transformation may improve the Gaussian distributions of regressed variables (e.g. Robinson & Williams 2005, p. 159), however, the log-transformed regression model did not improve the fit of our data or the normal distribution of the residuals. Regression of non-transformed variables resulted in the best model fit, and normality of the data and residuals met the assumptions of this analysis.

Rates of oxygen production expressed in carbon (C) units are converted assuming a photosynthetic quotient (PQ) of 1.2. This PQ falls within the lower range of PQ for ammonium-driven production (Laws 1991). We base our estimated PQ on reports of ammonium as the primary nitrogen source for productivity in the western end of LIS (Anderson & Taylor 2001), which agrees with the direct measurements of Oviatt et al. (1986) in the waters of nearby Narragansett Bay, Rhode Island.

RESULTS

Surface waters

Physical environment

Temporal trends. Temperature and salinity varied seasonally reaching their maxima in mid- to late-summer (Fig. 2). Surface temperatures ranged from a low of 2.5°C (May 2002) to highs in late August of 23.8°C in 2002 and 25.6°C in 2003. Variations in surface salinity lagged behind temperature, with lowest observed salinities through May (24.9) and June (23.8) of 2003 and highs in early October of 2002 (28.6) and 2003 (28.1). Interannual differences in average surface temperature throughout LIS for the 2 summers were not significant, however average surface salinity throughout LIS in the summer of 2003 was significantly lower than that in summer 2002 ($p < 0.001$, $n = 31$). Thermal stratification of the water column increased continuously during both summers, accompanied by continually decreasing bottom water oxygen concentrations

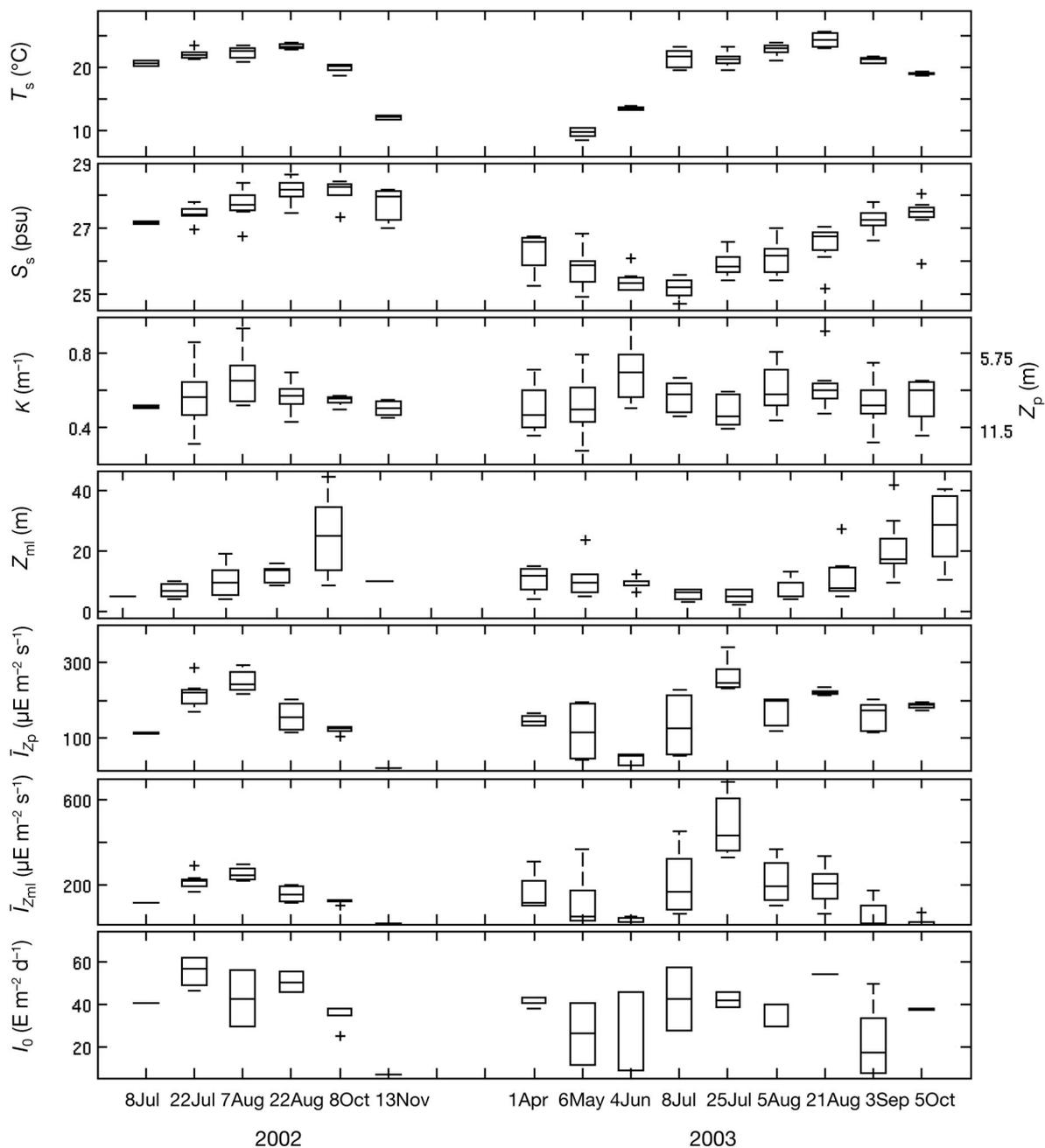


Fig. 2. Spatially averaged box-plots demonstrating seasonal (temporal) variation in surface (2 m) temperature (T_s , °C) and salinity (S_s , psu), light-attenuation (K , m^{-1}) and in photic depth (Z_p , m on right-hand ordinate), mixed-layer depth (Z_{ml} , m), average irradiance within photic zone and mixed layer (\bar{I}_{Z_p} and $\bar{I}_{Z_{ml}}$, $\mu E m^{-2} s^{-1}$), and incident irradiance averaged over each 2 to 3 d sampling period (I_0 , $E m^{-2} d^{-1}$). Lower and upper lines of each box = 25th and 75th percentiles of sample, respectively; distance between top and bottom of box: interquartile range; line through middle of box: sample median (when off-center indicates skewness); vertical lines extending above and below box show extent of rest of sample minus outliers: assuming no outliers, maximum and minimum of sample are upper and lower bars across ends of vertical lines; +: outliers

(not shown). Wind and storm events disrupted the pycnocline and alleviated the hypoxic conditions of bottom waters in late September to early October of 2002 and 2003. (Trends in bottom water oxygen concentrations for these times can be seen in results of the

CTDEP hypoxia cruises at http://dep.state.ct.us/wtr/lis/monitoring/lis_page.htm.)

Significant monthly variations were apparent in light attenuation in the water column (K), depth of the photic zone (Z_p), depth of the mixing layer (Z_{ml}), aver-

age daytime irradiance within the photic zone and mixing layer (\bar{I}_{Z_p} , $\bar{I}_{Z_{ml}}$), and incident daily irradiance (I_0) (Fig. 2). The highest \bar{I}_{Z_p} , $\bar{I}_{Z_{ml}}$ and I_0 occurred during the summer of both years. A seasonal increase in K (and a decrease in Z_p) was more apparent during the summer of 2002 than 2003 (Fig. 2). These descriptors of underwater irradiance (K and Z_p) exhibited steep, significant along-Sound gradients (see next subsection and Fig. 3) that confounded the apparent significance of average seasonal (monthly) trends (see Table 3). During the periods sampled, incident irradiance integrated over the day (I_0 ; Fig. 2) ranged from the mid-summer peak in late July (60 $E\ m^{-2}\ d^{-1}$) to a minimum in May 2003 (11 $E\ m^{-2}\ d^{-1}$). Observed photoperiods based on local incident irradiance data (not shown) ranged from 10 h (November 2002) to 17 h (June 2003).

Spatial trends. Spatial trends in temperature and salinity demonstrated small but consistent along-Sound gradients throughout the study, with lowest salinities and highest temperatures at the head (innermost western end) of the Sound (Fig. 3). These along-Sound gradients were strongest in mid-summer.

Significant along-Sound gradients in K (and Z_p) were also apparent throughout the study (see Table 3), with highest attenuation (0.9 to 1.0 m^{-1}) at the innermost station during mid-summer of 2002 and early and late summer of 2003. Throughout the study, K ranged from 0.5 to 1.0 m^{-1} at the innermost station and 0.3 to 0.6 m^{-1} at the outermost station, averaging $0.6 \pm 0.1\ m^{-1}$ for all irradiance profiles (Table 1). Photic zone depth (Z_p) averaged $8.7 \pm 2.1\ m$ for all observed irradiance profiles (Table 1) and resided within the depth of the upper mixed layer for approximately half of the observation period (average $Z_{ml} = 12.0 \pm 9.2\ m$). These values for Z_p and Z_{ml} compare well with respective ranges of 5 to 11 m and 4 to 15 m measured at Stn A4 by Anderson & Taylor (2001).

P-I parameters and pigments

Overall trends. Fig. 4 shows 9 representative *P-I* curves to demonstrate and compare variability in fitted *P-I* parameters (α^B and P_m^B). These examples were

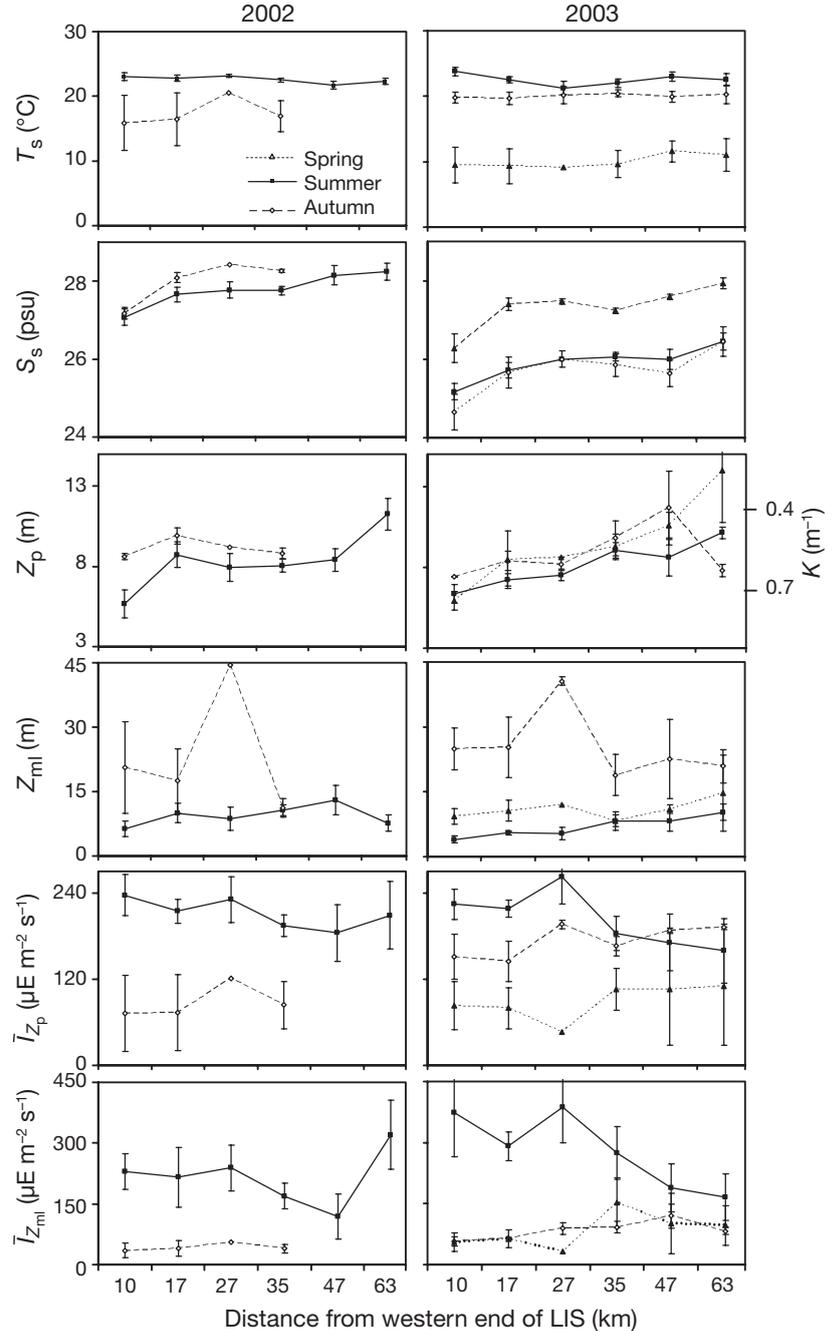


Fig. 3. Mean \pm SE interannual and spatial variation in surface temperature (T_s , $^{\circ}C$) and salinity (S_s , psu), photic depth (Z_p , m) and light attenuation (K , m^{-1} , on right-hand ordinate), mixed-layer depth (Z_{ml} , m) and average irradiance within photic zone and mixed layer (\bar{I}_{Z_p} and $\bar{I}_{Z_{ml}}$, $\mu E\ m^{-2}\ s^{-1}$) averaged during summer and autumn of 2002 and spring, summer and autumn of 2003. Outliers (>3 interquartile ranges) omitted

measured in the summers of 2002 and 2003 and autumn 2003 at 3 stations along the axis of cwLIS: inner (A4), mid (C1/2) and outer (H4) (Fig. 1). The *P-I* parameters did not vary consistently with space.

Across the entire data set (minus outliers) P_m^B demonstrated the lowest variability (range factor) com-

Table 1. Mean, standard deviation (SD), coefficient of variation for entire data set (CV), range, median and percentiles (minimum, 25%, median, 75%, maximum), number of samples (n), and range factors (x-fold) over entire sampling duration for variables: P - I parameters (α^B , P_m^B , $I_k = P_m^B/\alpha^B$), light-attenuation (K), photic depth (Z_p), mixed layer depth (Z_{ml}) and average irradiance in the photic zone (\bar{I}_{Z_p}) and mixed layer ($\bar{I}_{Z_{ml}}$). Range factors (x-fold) are also calculated for each season. Outliers (defined as 3 interquartile ranges from edge of interquartile range) omitted from estimates of fitted parameters. See 'Materials and methods' for parameter units

	α^B	P_m^B	I_k	K	Z_p	Z_{ml}	\bar{I}_{Z_p}	$\bar{I}_{Z_{ml}}$
Mean	10.9	1.3	132.6	0.6	8.7	12.0	168.6	178.9
SD	5.4	0.4	71.9	0.1	2.1	9.2	73.0	144.8
CV	0.5	0.3	0.5	0.2	0.2	0.8	0.4	0.8
Minimum	2.1	0.3	40.7	0.3	4.2	2.0	19.5	17.2
25 %	7.2	1.0	79.9	0.5	7.4	6.0	121.2	67.0
Median	10.3	1.2	113.2	0.6	8.4	9.1	188.1	126.3
75 %	14.1	1.4	172.5	0.6	9.6	15.0	220.0	272.6
Maximum	29.5	2.5	349.2	1.0	17.2	44.4	338.8	682.1
n	91	96	97	98	98	98	98	98
Range factor (x-fold): All	14	5	9	3	4	22	17	40
Summer 2002 (n = 23)	5	3	4	3	3	7	2	9
Summer 2003 (n = 30)	8	3	5	2	2	4	12	30
Autumn 2002 (n = 6)	10	2	5	1	1	5	7	4
Autumn 2003 (n = 13)	2	2	2	2	2	5	2	4
Spring 2003 (n = 7)	4	3	7	2	2	6	5	11

Table 2. Statistical descriptors (as in column 1 of Table 1) for chlorophyll (chl), phaeopigments (phaeo), phaeo:chl and community respiration (R_c) at surface, mid and bottom depths. Subscripts designate surface (s), mid (m) and bottom (b) depths. Units for chl and phaeo (except for phaeo:chl) are mg m^{-3} , units for R_c are $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$

	Chl _s	Chl _m	Chl _b	Phaeo _s	Phaeo _m	Phaeo _b	Phaeo:chl _s	Phaeo:chl _m	Phaeo:chl _b	R_{c_s}	R_{c_m}	R_{c_b}
Mean	6.9	3.0	1.7	3.5	2.3	1.9	0.7	0.9	1.5	1.4	0.8	0.7
SD	4.9	1.6	1.0	2.5	1.1	0.9	0.9	0.6	1.1	0.9	0.6	0.5
CV	0.7	0.5	0.6	0.7	0.5	0.5	1.2	0.7	0.7	0.6	0.7	0.7
Minimum	2.1	0.5	0.3	0.9	0.6	0.3	0.2	0.3	0.1	0.1	0.0	0.0
25 %	3.5	1.9	0.9	1.9	1.4	1.3	0.4	0.5	0.9	0.7	0.5	0.3
Median	5.6	2.9	1.8	2.7	2.1	1.6	0.5	0.7	1.2	1.4	0.7	0.6
75 %	7.6	3.7	2.5	4.6	2.6	2.5	0.7	1.3	1.6	1.9	1.2	1.0
Maximum	24.1	8.7	4.2	12.4	5.7	4.8	6.3	3.0	6.2	4.0	2.8	1.9
n	98	98	98	98	98	97	98	96	96	88	76	76
Range factor (x-fold): All	11	19	14	14	9	15	27	10	56	28	90	60
Summer 2002 (n = 23)	8	6	10	5	9	11	3	9	58	10	1	1
Summer 2003 (n = 30)	8	19	11	14	4	8	27	9	6	16	114	33
Autumn 2002 (n = 6)	2	5	10	3	4	12	3	2	4	2	16	30
Autumn 2003 (n = 13)	3	2	3	3	2	2	4	3	4	7	3	4
Spring 2003 (n = 7)	9	3	4	2	4	4	1	2	1	12	4	3

pared to chl and phaeo concentrations, α^B , I_k and R_c (Tables 1 & 2). Coefficients of variation for the averages over the entire data set were lowest for P_m^B and highest for chl and R_c , with α^B intermediate. The average coefficient of variation associated with the error in the fit of the P - I model (Eq. 2) for α^B (0.7) was almost 3 times greater than that of P_m^B (0.25). P_m^B averaged $1.3 \pm 0.4 \text{ mmol O}_2 [\text{mg chl}]^{-1} \text{ h}^{-1}$ (equivalent to $1.0 \pm 3.1 \text{ mmol C} [\text{mg chl}]^{-1} \text{ h}^{-1}$) and varied 5-fold. Chl averaged $6.9 \pm 4.9 \text{ mg m}^{-3}$ and varied 11-fold. α^B averaged $10.9 \pm 5.4 \text{ } \mu\text{mol O}_2 [\text{mg chl}]^{-1} \text{ h}^{-1}$ ($\mu\text{E m}^{-2} \text{ s}^{-1}$)⁻¹ (equivalent to $9.1 \pm 4.5 \text{ } \mu\text{mol C} [\text{mg chl}]^{-1} \text{ h}^{-1}$ [$\mu\text{E m}^{-2} \text{ s}^{-1}$]⁻¹) and

varied 14-fold. As expected, the range factor of model-fitted parameters and environmental variables was narrower for specific seasons (Tables 1 & 2).

In a multivariate ANOVA, comparisons varied significantly among sampled years (2002 vs. 2003) for α^B , R_c and I_k , but not for chl, phaeo or P_m^B (Table 3). Among summers only, ANOVA indicated significant interannual variation for α^B ($p < 0.001$), R_c ($p < 0.040$) and I_k ($p < 0.001$), but not chl, phaeo, or P_m^B . All P - I parameters and pigment concentrations varied significantly with month. Along the length of the Sound (by station) concentrations of chl and phaeo and rates of commu-

Table 3. A 3-way ANOVA for natural log-transformed photosynthetic parameters (α^B and P_m^B), community respiration (R_c), chlorophyll (chl), phaeopigments (phaeo), I_k , and irradiance variables (K and Z_p , Z_{ml} , \bar{I}_{Z_p} and $\bar{I}_{Z_{ml}}$) measured in surface waters along the main transect of the Sound by station ($n = 8$), by month ($n = 8$) and by year ($n = 2$). Significant Levene's test ($p < 0.001$) rejected equality of the variances for all ANOVA tests, therefore significant differences were checked with 1-way ANOVA and Welch & Brown-Forsyth robust tests of equality of means. The only multivariate ANOVA statistics that did not hold in the 1-way ANOVA (hence deemed non-significant) were monthly variation in K and Z_p and spatial variation for Z_{ml} (*italicized* showing both results). Values in **boldface**: significant at $p < 0.05$ level. Outliers omitted

Source	$\ln \alpha^B$	$\ln P_m^B$	$\ln R_c$	$\ln \text{Chl}$	$\ln \text{Phaeo}$	$\ln I_k$	$K \& Z_p$	Z_{ml}	$\ln \bar{I}_{Z_{ml}}$	$\ln \bar{I}_{Z_p}$
Site	0.62	0.08	<0.001	<0.001	<0.001	0.90	<0.001	<i><0.001/0.24</i>	0.32	0.98
Month	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<i><0.01/0.08</i>	<0.001	<0.001	<0.001
Year	0.02	0.08	<0.001	0.31	0.28	0.03	0.69	0.46	0.54	0.74
Site \times Month	0.29	0.03	0.38	0.33	0.09	0.39	0.93	0.02	0.63	0.97
Site \times Year	0.66	0.02	0.44	0.56	0.03	0.30	0.62	0.57	0.58	0.93
Month \times Year	0.10	0.02	<0.01	0.41	0.16	0.22	0.63	0.95	0.87	0.53
Site \times Month \times Year	0.29	0.25	0.28	0.50	0.10	0.53	0.99	0.31	0.99	0.89

nity respiration (R_c) varied significantly. However, ANOVA tests revealed no significant spatial variability in α^B , P_m^B , or I_k (Table 3).

Temporal trends. Spatially averaged surface chl and phaeo concentrations and $P-I$ parameters (P_m^B , α^B and I_k) increased significantly during spring and summer seasons (Fig. 5, Table 3). Chl and phaeo concentrations peaked in late July to early August of 2002 and 2003 and in late spring (May) of 2003. (Note that our cruises did not sample December through March, thus missing a possible winter–spring bloom.) P_m^B increased significantly during both summer periods, with maxima in late August of 2002 and 2003. Although monthly trends in α^B were less clear-cut than in chl and P_m^B , α^B did peak and correlate with P_m^B ($r = 0.380$, $p < 0.001$, $n = 90$; see later subsection) and varied significantly by month (Table 3) due to the extremes of summer maxima (June and August 2003) and an autumn minimum (November 2002). I_k varied significantly throughout the observation period. A seasonal peak was more apparent during the summer of 2003; however, the maximum I_k was observed in November 2002. R_c increased significantly during late summer to early autumn ($p < 0.0001$). The maximum ratio of phaeo:chl (not shown) was detected in the following sampling period (2 wk) after the summer chl peaks.

Spatial trends. Chl and phaeo decreased seaward along the length of LIS consistently during each sampling period, as demonstrated by seasonal averages (Fig. 6). During the height of each summer bloom (late July to early August), maximum chl concentrations at the head of the Sound decreased seawards 5-fold (2002) to 7-fold (2003) toward the outermost station, in central LIS. This gradient was either diminished or not evident during sampled periods of low biomass. In contrast, variability was insignificant along the Sound for biomass-specific $P-I$ parameters (P_m^B , α^B , and I_k) on most cruises (Fig. 6, Table 3).

Inter-relationships among $P-I$ parameters, pigments and physical environment

$P-I$ parameters versus chl. Chl measured in surface waters was not significantly correlated with α^B or P_m^B for the entire data set (Table 4). However, changes in the relationships between chl and $P-I$ parameters could be identified for some seasons (Fig. 7). Different clusters of P_m^B with chl were apparent, particularly during late summer and spring (Fig. 7A). In contrast, seasonal groups of α^B with chl were less apparent due to the overlapping of clusters, which distinguished high chl periods (late summer and spring) from low chl periods (early summer and autumn; Fig. 7B). The relationship between α^B and P_m^B varied with season (Fig. 7C). The slopes of P_m^B versus α^B for each season were significant but indistinguishable from each other except for a 2-fold increase in late summer (Fig. 7C).

$P-I$ parameters versus irradiance variables. Correlations between $P-I$ parameters, chl, temperature, and irradiance values are summarized in Table 4. Of interest is a significant correlation between α^B and the depth of the mixed layer (Z_{ml}), but not with the depth of the 1% light level (Z_p). In contrast, P_m^B correlated significantly with Z_p but not with Z_{ml} .

Average daytime irradiance in the photic zone (\bar{I}_{Z_p}) and in the mixed layer ($\bar{I}_{Z_{ml}}$) were comparable when averaged across the study (Table 1), however $\bar{I}_{Z_{ml}}$ was more variable (Table 1) due to higher values during periods of increased mixed layer depth (e.g. autumn turnover). Both of these measures of environmental light availability were 21 to 26% higher than the overall average physiological saturation intensity, I_k . I_k was significantly correlated with both \bar{I}_{Z_p} , $\bar{I}_{Z_{ml}}$, as well as α^B , but not with P_m^B (Table 4).

The positive correlation of K with phytoplankton biomass for the entire data set (Table 4) was primarily attributable to high biomass periods during summer

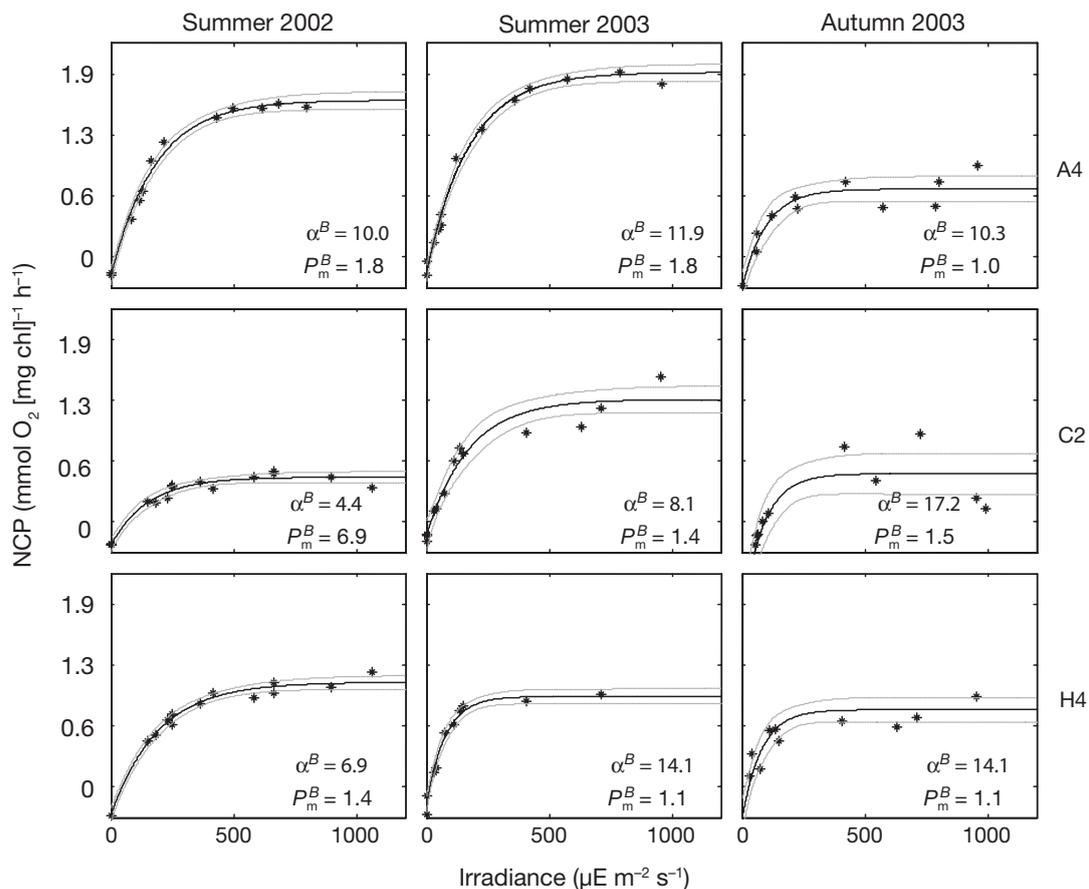


Fig. 4. Fitted P - I curves and derived photosynthetic parameters (α^B ; $\mu\text{mol O}_2 [\text{mg chl}]^{-1} \text{h}^{-1} [\mu\text{E m}^{-2} \text{s}^{-1}]^{-1}$ and P_m^B ; $\text{mmol O}_2 [\text{mg chl}]^{-1} \text{h}^{-1}$) measured for surface-water samples collected at 3 stations along main axis of LIS (Stns A4, C2, and H4) during summers of 2002 and 2003, and autumn 2003. NCP: net community O_2 production

($r = 0.500$, $p < 0.001$, $n = 63$) and spring ($r = 0.781$, $p < 0.008$, $n = 9$). Note however, that chl on average only explains one quarter ($r^2 = 0.26$) of the variance in K (Table 4).

P - I parameters versus temperature. The relationship between P_m^B and temperature demonstrated considerable scatter (Fig. 8A). There is an upper envelope for variation in P_m^B with temperature, similar to that proposed for growth rate (μ) by Eppley (1972). However, the upper values here exceed the Eppley limit when P_m^B is converted to μ using $PQ = 1.2$ and adjusted for photoperiod. Similar disparities have been reported elsewhere (Brush et al. 2002).

Community respiration rates (R_c)

In the upper mixed layer the volumetric rate of community respiration, R_c , ranged from almost undetectable (0.06) to $4.0 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$, with an average of $1.4 \pm 0.9 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ (Table 2). Although beyond the ± 3 interquartile range criterion used to

omit outliers, a replicated maximum respiration rate of $8.9 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$ was observed. R_c demonstrated a significant gradient along the length of LIS in all seasons (Fig. 6, Table 2), with significantly higher rates at the head (western end) of the Sound in late July to early August of 2002 and 2003. R_c showed a weak non-linear relationship with temperature (Fig. 8B).

The relationship between R_c and chl concentration sampled in surface waters was tested among individual sampling trips, individual sampled stations, and for the combined data set. The slopes of the relationship between R_c and chl were consistent for individual sampling trips (Fig. 9) and stations located along the main axis of the Sound, displaying no obvious temporal or spatial trends. However, one-quarter of these individual correlations did not exceed an r of 0.5. These weak relationships between R_c and chl for individual sampling trips and stations are attributable to the low sample number (n) and small range of chl measured among these subsets. For the combined data set, a relationship between R_c and chl concentration in surface waters was highly significant ($r = 0.60$, $p < 0.001$,

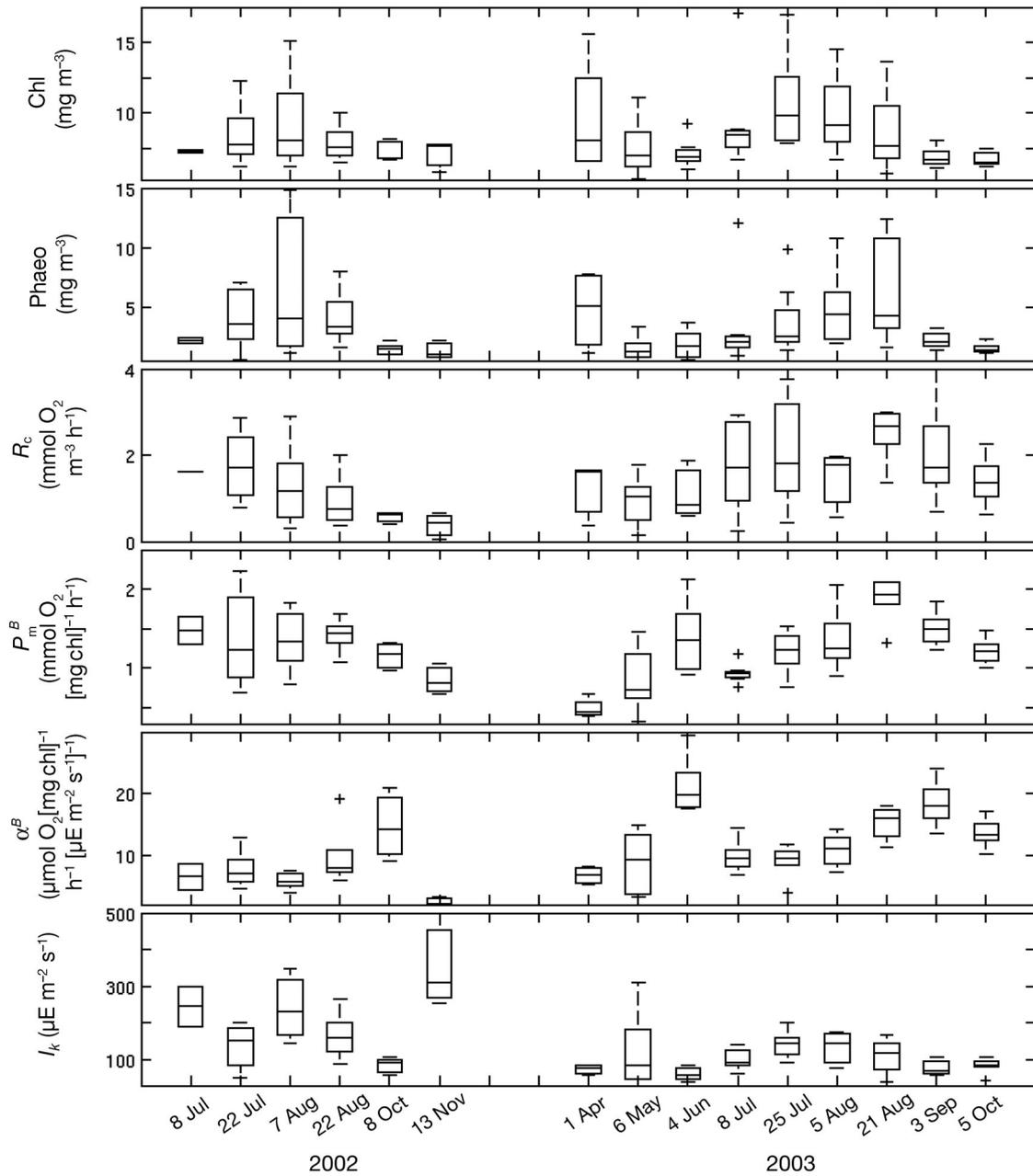


Fig. 5. Spatially averaged box-plots demonstrating seasonal variation in surface phytoplankton stock (chl), phaeopigments (phaeo), and photosynthetic parameters: R_c , P_m^B , α^B and I_k throughout summer and autumn of 2002 and spring, summer, and autumn of 2003. See Fig. 2 legend for further details

$n = 87$; Fig. 9). The overall slope of this relationship was $0.09 \pm 0.02 \text{ mmol O}_2 [\text{mg chl}]^{-1} \text{ h}^{-1}$ with a y -intercept of $0.39 \pm 0.10 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$.

The product of the slope of the above relationship and chl measured at each sampled station was used to estimate the daytime respiration associated with algae, R_a . The mean and 95% confidence intervals for the ratio $R_a:R_c$ (0.51 ± 0.08) suggests that chl was associated with about half of the measured daytime plankton community respiration in surface waters.

Mid and bottom waters

On average for all stations, concentrations of both chl and phaeo at mid depths were one-half of those measured at the surface, while chl and phaeo at bottom depths were one-third average surface values. Discrete measurements of chl at mid and bottom depths ranged from 2 to 180% of that measured at the surface, similar to the 7 to 100% observed at Stn A4 in LIS by Anderson & Taylor (2001). At mid and bottom depths,

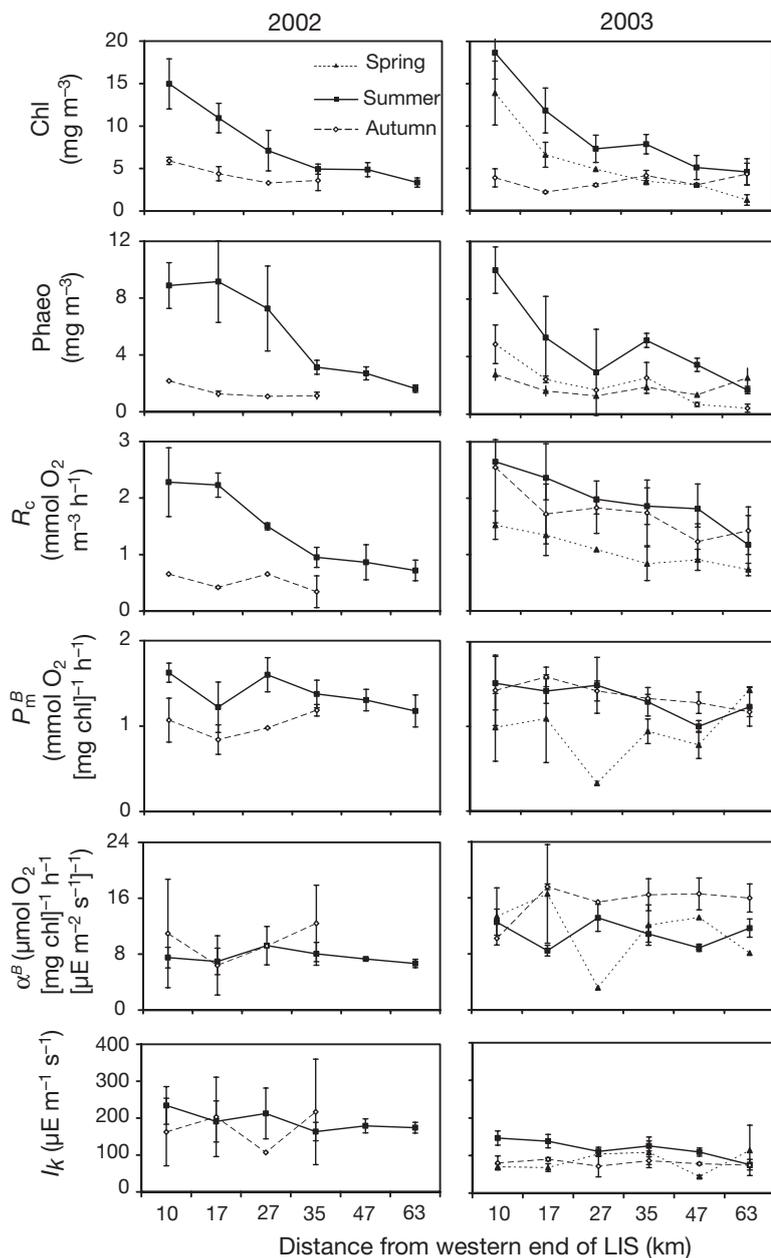


Fig. 6. Mean \pm SE interannual and spatial variation in surface phytoplankton stock: chl, phaeopigments: phaeo, community respiration: R_c , and photosynthetic parameters: P_m^B , α^B and I_k along main axis of central and western LIS averaged during summer and autumn of 2002 and spring, summer and autumn of 2003. Outliers (>3 interquartile ranges) omitted

chl averaged 3.0 ± 1.6 and 1.7 ± 1.0 mg m^{-3} and varied 19- and 14-fold over all samples, while phaeo averaged 2.3 ± 1.1 and 1.9 ± 0.9 mg m^{-3} and varied 9- and 15-fold (Table 2). The phaeo:chl ratio increased with increasing depth, with averages of 0.9 ± 0.6 and 1.5 ± 1.1 and ranges of 10- and 56-fold at mid and bottom depths, respectively (Table 2). Overall, both chl and phaeo at the surface were significantly correlated with their values measured in mid and bottom samples (Table 5).

Chl and phaeo were also significantly correlated at mid and bottom depths (Table 5). Chl and phaeo at mid and bottom depths demonstrated spatial gradients similar to those observed in surface waters.

R_c at mid and bottom depths of the water column ranged from undetectable to 2.8 and 1.9 $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$, with respective averages of 0.8 ± 0.6 and 0.7 ± 0.5 $\text{mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$. These rates were typically less than half of that measured at the surface (Table 2). R_c at the surface was not correlated with R_c at mid or bottom depths over time or space. R_c at mid and bottom depths however, were significantly correlated (Table 5), attributable primarily to a highly significant relationship during summer. No obvious spatial gradients in R_c at mid and bottom depths were observed along the main axis of the Sound.

DISCUSSION

Temporal and spatial variation in physiological parameters (α^B , P_m^B , R_c) and pigments

Phytoplankton pigment concentrations and photosynthetic parameters demonstrated high variability in time (seasons) and space (along-Sound gradients) in LIS. The maxima in pigments, P_m^B , and R_c at the head of the Sound during mid summer (Fig. 5) resulted in strong decreasing gradients of these variables and parameters along the main axis of LIS. The sustained, maximum summer chl (24.1 mg m^{-3} ; Table 2) was comparable to that measured by Riley (1959; $\sim 23 \text{ mg m}^{-3}$) and Anderson & Taylor (2001; 28.2 mg m^{-3}), all measured in the western end of LIS during the summer. Our average chl in LIS compares well with the annual average chl measured in surface waters of other eutrophic systems such as mid-Chesapeake Bay (Harding et al. 2002), upper Narragansett Bay (Oviatt et al. 2002) and Suisun Bay channel of San Francisco Bay (Cole & Cloern 1984). We did not sample during the winter-spring season, suggesting that a more complete annual average for LIS might be even higher with the inclusion of non-sampled winter bloom values.

Maximum estimates of P_m^B and α^B in LIS, converted to units of carbon for comparison with ^{14}C , are 1.5 and 3 times the maximum measured in some other produc-

tive systems such as the Chesapeake and Delaware Bays (Harding et al. 1985, 1986). Converted maxima of P_m^B measured in LIS (~ 2.1 mmol C [mg chl] $^{-1}$ h $^{-1}$) matched the theoretical maximum (2.1 mmol C [mg chl] $^{-1}$ h $^{-1}$) calculated by Falkowski (1981). However

converted maxima of α^B (~ 0.02 mmol C [mg chl] $^{-1}$ h $^{-1}$ [$\mu\text{E m}^{-2} \text{s}^{-1}$] $^{-1}$) was more than 6 times the theoretical maximum (0.003 mmol C [mg chl] $^{-1}$ h $^{-1}$ [$\mu\text{E m}^{-2} \text{s}^{-1}$] $^{-1}$) calculated by Platt & Jassby (1976), even after removal of weakly fitted P - I curves and exclusion of out-

Table 4. Bivariate Pearson correlation coefficients for P - I parameters, community respiration, surface temperature (T) and chlorophyll (chl), average chlorophyll in the euphotic zone (chl_{avg}), and irradiance variables (K , Z_p , Z_{ml} , $\bar{I}_{Z_{\text{ml}}}$ and \bar{I}_{Z_p}). Correlation coefficient (r), significance (p), and number of samples (n) are shown. Correlations in **boldface** are significant at $p < 0.05$ level (2-tailed). Outliers omitted

	α^B	P_m^B	I_k	R_c	T	Chl	Chl_{avg}	K	Z_p	Z_{ml}	$\bar{I}_{Z_{\text{ml}}}$	\bar{I}_{Z_p}
P_m^B												
r	0.380											
p	<0.001											
n	90											
I_k												
r	-0.650	0.143										
p	<0.001	0.167										
n	90	95										
R_c												
r	0.071	0.287	-0.083									
p	0.527	0.007	0.446									
n	82	87	87									
T												
r	0.042	0.518	0.217	0.305								
p	0.692	<0.001	0.033	0.004								
n	91	96	97	88								
Chl												
r	-0.171	0.058	0.279	0.463	0.164							
p	0.104	0.573	0.006	<0.001	0.106							
n	91	96	97	88	98							
Chl_{avg}												
r	-0.263	-0.090	0.251	0.406	0.100	0.894						
p	0.012	0.381	0.013	<0.001	0.328	<0.001						
n	91	96	97	88	98	98						
K												
r	0.177	0.254	0.085	0.206	0.127	0.515	0.450					
p	0.094	0.013	0.408	0.054	0.212	<0.001	<0.001					
n	91	96	97	88	98	98	98					
Z_p												
r	-0.067	-0.235	-0.111	-0.231	-0.218	-0.485	-0.434	-0.876				
p	0.528	0.021	0.281	0.030	0.031	<0.001	<0.001	<0.001				
n	91	96	97	88	98	98	98	98				
Z_{ml}												
r	0.282	0.104	-0.256	-0.096	-0.018	-0.325	-0.360	-0.229	0.242			
p	0.007	0.315	0.011	0.375	0.858	<0.001	<0.001	0.023	0.016			
n	91	96	97	88	98	98	98	98	98			
$\bar{I}_{Z_{\text{ml}}}$												
r	-0.345	0.046	0.301	0.284	0.238	0.378	0.378	-0.079	-0.038	-0.517		
p	<0.001	0.656	0.003	0.007	0.018	<0.001	<0.001	0.440	0.713	<0.001		
n	91	96	97	88	98	98	98	98	98	98		
\bar{I}_{Z_p}												
r	-0.278	0.326	0.371	0.380	0.487	0.341	0.324	-0.011	-0.108	-0.076	-0.637	
p	0.008	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.916	0.291	0.456	<0.001	
n	91	96	97	88	98	98	98	98	98	98	98	
I_0												
r	-0.284	0.334	0.393	0.399	0.526	0.362	0.343	0.072	-0.109	-0.190	0.654	0.949
p	0.006	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.483	0.285	0.061	<0.001	<0.001
n	91	96	97	88	98	98	98	98	98	98	98	98

Table 5. Bivariate Pearson correlation coefficients for chlorophyll (chl) and phaeopigment (phaeo) concentrations, and rates of community respiration (R_c) in samples collected from the surface, mid and bottom depths. Subscripts designate surface (s), mid (m) and bottom (b) sample depths. Correlation coefficients (r), significance (p) and number of samples (n) are shown. Correlations in **boldface** are significant at $p < 0.01$ level (2-tailed). Outliers omitted

	Chl _s	Phaeo _s	R_{c_s}	Chl _m	Phaeo _m	R_{c_m}	Chl _b	Phaeo _b
Phaeo _s								
r	0.728							
p	<0.001							
n	98							
R_{c_s}								
r	0.463	0.444						
p	<0.001	<0.001						
n	88	88						
Chl _m								
r	0.562	0.290	0.196					
p	<0.001	0.004	0.067					
n	98	98	88					
Phaeo _m								
r	0.514	0.550	0.287	0.546				
p	<0.001	<0.001	0.007	<0.001				
n	98	98	88	98				
R_{c_m}								
r	0.158	0.222	0.175	0.026	0.130			
p	0.172	0.053	0.154	0.821	0.261			
n	76	76	68	76	76			
Chl _b								
r	0.339	0.167	-0.013	0.755	0.318	0.138		
p	<0.001	0.101	0.902	<0.001	<0.001	0.233		
n	98	98	88	98	98	76		
Phaeo _b								
r	0.336	0.182	0.035	0.477	0.450	0.001	0.666	
p	<0.001	0.074	0.747	<0.001	<0.001	0.996	<0.001	
n	97	97	87	97	97	75	97	
R_{c_b}								
r	-0.071	0.062	0.047	0.008	0.122	0.484	0.302	0.346
p	0.542	0.596	0.702	0.946	0.295	<0.001	0.008	0.002
n	76	76	69	76	76	62	76	75

liers (see 'Materials and methods'). The mean of α^B ($0.009 \text{ mmol C [mg chl]}^{-1} \text{ h}^{-1} [\mu\text{E m}^{-2} \text{ s}^{-1}]^{-1}$) was within the same order of magnitude as theory, but still higher. High measurements of α^B have also been observed in other studies (Platt & Jassby 1976, Malone & Neale 1981, Kelly & Doering 1997).

Seasonality in α^B was not as distinct as P_m^B ; α^B increased during each summer and was significantly higher in 2003, but lacked any defined spatial and temporal trends like those of P_m^B and chl (Figs. 5 & 7). Although variability of α^B in LIS during summers decreased (i.e. 5- to 8-fold ranges versus 14-fold overall; Table 1), α^B variability was still at least double that of P_m^B during individual seasons as well as over the duration of the study (Table 1). Higher variability in α^B contrasts with that reported in diel (MacCaull & Platt 1977, Prézélin & Sweeney 1977), daily (Cote & Platt 1983) and seasonal (Platt & Jassby 1976) $P-I$ studies,

where range factors of α^B were similar to or less than P_m^B . In those studies, however, $P-I$ parameters did not necessarily correlate temporally, as was observed in the present study. Relatively high variability in the fit of α^B is not unusual. Aalderink & Jovin (1997) measured similar disparities in the fit of $P-I$ parameters across 8 model types for oxygen production and consumption in light and dark bottle incubations, whether these parameters were fitted using net or gross rates of primary production. Higher variability in the fit of $P-I$ parameters does not appear to result from use of the O_2 method. This was demonstrated by similar variability in the curve-fits of our $P-I$ parameters to that calculated using both O_2 and ^{14}C in Massachusetts Bay (Kelly & Doering 1997). Importantly, Kelly & Doering (1997) demonstrated that imprecise measures of α^B do not largely influence calculations of integrated production, yet Aalderink & Jovin (1997) stressed the impor-

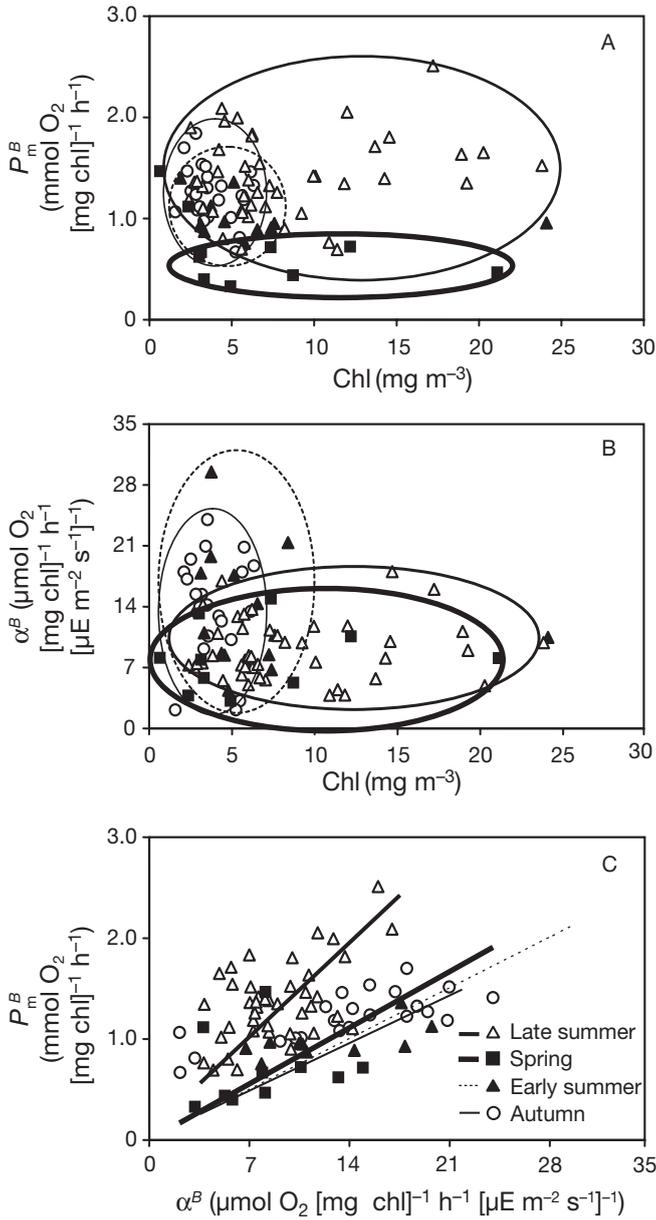


Fig. 7. Seasonal relationships between (A) maximum photosynthetic rate (P_m^B) and chl, (B) photosynthetic efficiency (α^B) and chl, and (C) P_m^B and α^B for all sample data. Both sample years combined and reported by season, which are indicated by ellipses containing seasonal clusters of data in (A) and (B), and by regression lines for each season in (C). Overlapping ellipses in (A) distinguish similarities in relationship between P_m^B and chl during low chl periods of autumn (thin line) and early summer (dotted line), from high chl–high P_m^B during late summer (medium line) and high chl–low P_m^B during spring (dark line). Pairs of overlapping ellipses in (B) indicate fewer seasonal differences in relationship between α^B and chl during low chl periods (autumn and early summer) and high chl periods (late summer and spring). Seasonal variations in relationship between α^B and P_m^B are demonstrated by regression lines for each season in (C), where highest slope was in late summer ($r = 0.54$), decreasing to spring ($r = 0.84$), early summer ($r = 0.50$), and autumn (lowest slope, $r = 0.75$).
Outliers omitted

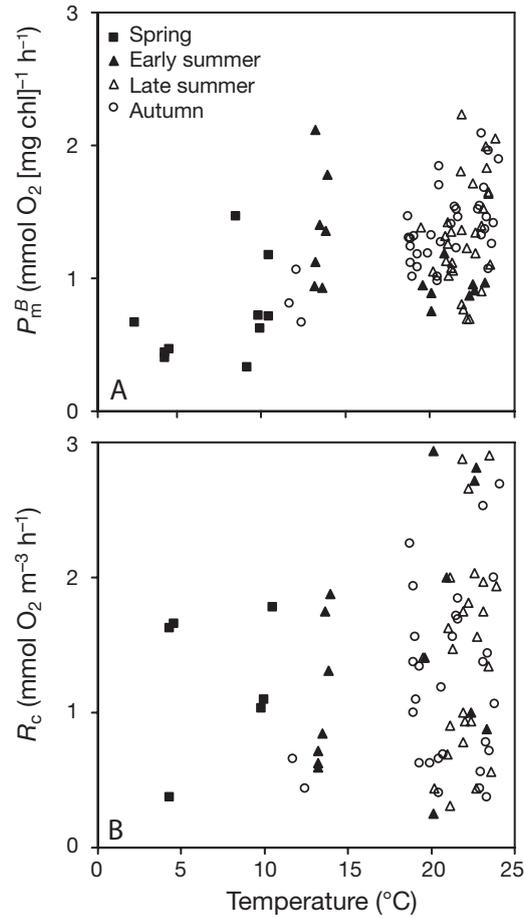


Fig. 8. Temperature versus (A) maximum photosynthetic rate (P_m^B) and (B) community respiration (R_c) for all sample data. Outliers omitted

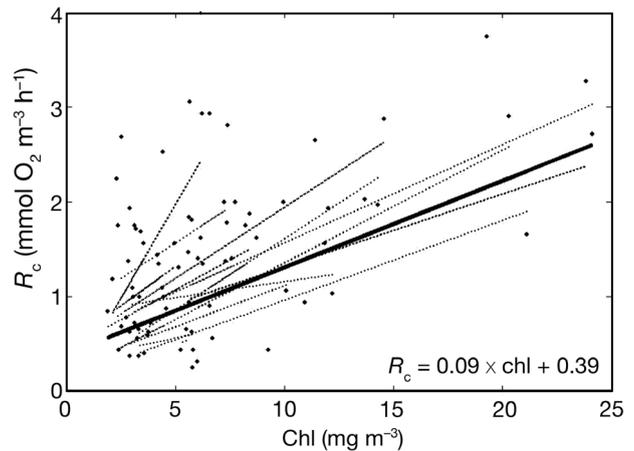


Fig. 9. Relationship between community respiration (R_c) and chlorophyll (chl) concentration of surface-water samples measured on each sampling trip (dotted lines) and for all data (continuous line). Overall slope calculated in weighted Model II regression was 0.09 ± 0.02 mmol O_2 [mg chl] $^{-1}$ h $^{-1}$ with an intercept of 0.39 ± 0.10 mmol O_2 m $^{-3}$ h $^{-1}$ ($r = 0.60$, $p < 0.001$, $n = 87$). Slopes for most individual sampling trips were similar to overall slope, although not all were significant

tance of precise parameter estimation when investigating their individual dependencies on environmental conditions.

The average R_c in LIS for all seasons and stations ($1.4 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$) was more than twice the maximum rates measured in surface waters of western LIS by Riley (1959), although his method employed 3 to 4 d dark incubations. Our results compared favorably to more recent studies in LIS. The maximum 24 h dark incubation measured in surface waters at the head of LIS by Anderson & Taylor (2001) was equivalent to $2.1 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$. The average for 8 h incubations in surface waters throughout central and western LIS by Welsh & Eller (1991) was $\sim 1.9 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$. Our results also compare well with those of other eutrophic systems, such as the average measured during spring to autumn at the head of a eutrophic Danish estuary ($1.8 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$; Jensen et al. 1990). The overall average rate for LIS is ~ 3 times the global geometric mean ($9.1 \text{ mmol C m}^{-3} \text{ d}^{-1}$; $n \approx 700$) and 1.6 times the arithmetic mean ($17.8 \text{ mmol C m}^{-3} \text{ d}^{-1}$) for 21 estuarine systems (Hopkinson & Smith 2005, p. 133, 134). The maximum rate of respiration measured in the present study ($8.9 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$) is among the highest reported, equating to 25 and 12 times these global geometric and arithmetic means.

Numerous ecological factors may contribute real variation in the parameters, such as mean cell size (Platt & Jassby 1976), nutrient availability (Lohrenz et al. 1993), changes in community structure associated with episodic physical events and growth conditions (Cote & Platt 1983, Forbes et al. 1987, Macedo et al. 2001), variation in the quantum yield and light trapping capacity of the resident phytoplankton community (Sosik & Mitchell 1995), or shifts in the fraction of photosynthetically produced reductants allocated to carbon fixation (Behrenfeld et al. 2004). Contribution of these factors as sources of variability in P - I parameters is not within the scope of the present study. We are able however, to explore the relationship between the variability of photosynthetic parameters, pigments, light and physics in the water column.

Relationships among photosynthetic parameters, pigments, light and water-column physics

Seasonal variability in chl and P - I parameters presumably result from varied responses of the phytoplankton community to changing conditions of temperature, light, water column structure and nutrients. Our data include a number of relevant descriptors of the photosynthetic environment: incident irradiance (I_0), light attenuation (K), and depth and average irradiance of the photic zone (Z_p , \bar{I}_{Z_p}), and of the mixed

layer (Z_{ml} , $\bar{I}_{Z_{ml}}$). The covariance of chl, P_m^B and α^B with all or several of these descriptors (Table 4) affirms and quantifies the obvious importance of light in determining chl and photosynthesis in LIS. Summer increases in chl with I_0 and stratification (as Z_{ml}) were also seen at Stn A4 by Anderson & Taylor (2001) during 1992 and 1993.

P_m^B covaried with both T_s and I_0 . It was not possible however, to distinguish between the importance of I_0 and T_s in the prediction of P_m^B , since day-to-day variability in both obscured any seasonal offset. Significant relationships between P_m^B and T were also found by Cote & Platt (1983), Behrenfeld & Falkowski (1997) and Macedo et al. (2001). In contrast, Gaxiola-Castro et al. (1999) did not observe a relationship between P_m^B and T , or nutrient concentrations. They did report a non-linear relationship between P_m^B and stratification of the water column, implying complex interactions of P_m^B with light, nutrients and water-column structure. Despite observed relationships between P_m^B and T , Cote & Platt (1983), Cullen et al. (1992) and Behrenfeld & Falkowski (1997) emphasized that factors other than temperature are responsible for variability in P_m^B , such as light acclimation. The scatter in our relationship of P_m^B to T in LIS (Fig. 8) suggests that temperature may not promote blooms directly (i.e. physiologically), but rather may play a more important role via increased stratification of the water column. Furthermore, our calculations of growth rate based on P_m^B offer another example of productivity data that exceed the Eppley temperature curve (Brush et al. 2002). Clearly, the Eppley temperature-dependent growth model is not an accurate predictor of maximum phytoplankton photosynthesis in LIS.

Both Riley (1959) and Anderson & Taylor (2001) stressed the importance of stratification and increased light availability to the progression of the summer to autumn period of increased productivity in LIS. As pointed out by Anderson & Taylor (2001), the variation in underwater irradiance is controlled more by I_0 than water clarity, K . This importance of I_0 is supported by increases in P_m^B and chl during the summer, despite increased self-shading indicated by parallel increases in phytoplankton biomass and K along the axis of LIS.

Unlike P_m^B , α^B was not correlated with temperature, but as expected α^B was inversely correlated with depth and light availability of the mixed layer (Z_{ml} and $\bar{I}_{Z_{ml}}$). This suggests that variability in α^B may be associated with adaptation of phytoplankton communities to significant changes in the light regime associated with the structure of the water column. The dependence of α^B on light levels and efficiency of light harvesting by resident phytoplankton communities of LIS is discussed using the derived parameter I_k .

$I_k (= P_m^B : \alpha^B)$ characterizes physiological adaptations to the environment (Beardall & Morris 1976) and growth potential (Prézelin & Matlick 1980) of algal populations. Average I_k in LIS ($132 \pm 72 \mu\text{E m}^{-2} \text{s}^{-1}$) was similar to values measured in other coastal regions of relatively shallow mixed layers, such as the range and average measured in Chesapeake and Delaware Bays (Harding et al. 1986). The relatively high values of I_k in LIS indicate that phytoplankton communities were adapted to high irradiances (i.e. light-adapted), according to the criteria of Steeman Nielsen & Hansen (1959) and Ichimura (1960).

Comparison of I_k with the amount of available *in situ* irradiance ($\bar{I}_{Z_{ml}}$) has been used to indicate how phytoplankton communities adapt to variations of irradiance in a hydrographically variable water column (Figueiras et al. 1994, 1998). Typically, I_k is expected to decrease with high chl (i.e. decreased light availability due to self-shading should lead to lower I_k through shade adaptation). Yet, in LIS, I_k increased with increasing chl and I_0 during peaks in productivity, and covaried with K along the length of LIS. Mean irradiance levels in the photic zone (\bar{I}_{Z_p}) and the mixed layer ($\bar{I}_{Z_{ml}}$) were only 21 and 26% higher than average I_k . The agreement between available light and I_k despite relatively high light attenuation suggests that LIS phytoplankton are not limited (nor photoinhibited) by light, and hence may be effectively adapted to their light regime much of the time, perhaps even for maximal rates of productivity.

We tested for seasonal variability in I_k utilizing the overall significant relationship between observations of P_m^B and α^B compiled for spring, early and late summer, and autumn seasons. The slope of the regression of P_m^B to α^B (Fig. 7C), did not differ significantly among spring, early summer and autumn, but increased 2-fold during late summer of both sampled years. This increase in I_k during late summer results from the asymmetries in the relationships of these P - I parameters to chl, whereby P_m^B increased more rapidly during late summer in relation to both chl and α^B (Figs. 7A, B).

Nutrients have not been included in this paper. Strong gradients in surface chl and P_m^B that decrease with increasing distance from the western end of LIS may implicate the influence of nutrients as well as salinity and temperature structure. In addition to higher stratification, nutrients in the waters at the head of LIS promote high productivity and chl in surface waters. Riley (1959) reports similar spatial gradients in chl and nutrients for inner, mid and outer regions of LIS. Additionally, seasonal blooms were accompanied by decreases in inorganic forms of nitrogen and phosphorus during present (CTDEP data, not shown) and previous studies (Riley 1959, Anderson & Taylor 2001), indicating uptake of available nutrients by phytoplankton. Al-

though nutrients were undetectable during peak concentrations of chl, the breakdown in stratification with storms in September of 2002 and 2003 promptly replenished surface nutrient (and bottom-water oxygen) concentrations (CTDEP data, not shown), as was also observed by Anderson & Taylor (2001).

Respiration

Surface waters

The rate of plankton-community respiration (R_c) measured in the surface mixed layer of LIS correlated significantly with chl and P_m^B (Table 4, Fig. 9), particularly during summer at the western end of the Sound. Chl explained more than twice as much variance in R_c than in P_m^B . We used the slope of the regression of R_c on chl to estimate a rate of daytime 'algal-related' respiration, R_a (i.e. algal respiration and microbial respiration associated with algal exudates). The y -intercept is a constant that represents respiration not associated with chl, or non-algal-related respiration (e.g. heterotrophic oxidation of detrital material), also referred to as non-phytoplankton or background respiration by Cohen (1990) and Jensen et al. (1990).

The overall slope of the relationship between R_c and chl was $0.09 \pm 0.02 \text{ mmol O}_2 [\text{mg chl}]^{-1} \text{ h}^{-1}$, where chl explained 37% of the variation in R_c (Fig. 9). This overall relationship did not differ significantly from the average for relationships tested across individual sampling trips and stations. The correlation between R_c and chl for the most eutrophic station at the western end of the Sound (A4) was especially strong and had the same slope ($0.09 \pm 0.03 \text{ mmol O}_2 [\text{mg chl}]^{-1} \text{ h}^{-1}$; $r = 0.83$). This region is likely to receive higher inputs of allochthonous dissolved organic carbon, which might fuel increased rates of non-algal respiration. However, the R_c versus chl slope at this station was consistent with the overall slope, and with the slopes of most individual sampling trips. Further, no temporal or spatial trends were observed in this relationship, although low sample numbers and small ranges of chl observed during individual trips and at individual stations meant that these regressions were not all significant. Therefore we estimate R_a for all stations using the slope of the combined regression.

The average of R_a as a fraction of observed R_c indicated that algal-related respiration constitutes 43 to 60% of daytime community respiration. Our estimates of the proportion of R_a to R_c overlap the range of 50 to 65% reported by studies in LIS (Riley 1959), the North Atlantic (Siegel et al. 2002, Marra & Barber 2004), and a eutrophic Danish estuary (Jensen et al. 1990). This estimate is an upper limit for the contribution of phyto-

plankton to pelagic respiration in the water column during this study, because R_a represents not only algal respiration but also the respiration of microbial communities directly related to phytoplankton (e.g. exudates, lysis and senescence). We are not able to separate the indirect, algal-related respiratory processes that would permit a more accurate measure of actual phytoplankton respiration.

In the P - I literature, algal respiration rates are commonly assumed to be a fraction of P_m^B for the calculation of net primary production (Riley 1946, Steemann Nielsen & Hansen 1959, Cole & Cloern 1984, Langdon 1993 and references therein). This appears to be based on convenience, as there is little reason to expect a relationship with a statistical physiological parameter that is independent of the level of actual productivity *in situ*. Previous estimates of this respiration relationship range very widely: 3 to 7% (Harris & Piccinin 1977), 6% (Holligan et al. 1984, Jensen et al. 1990), 5 to 10% (Laws 1975), and 10% (range of 5 to 24%; Steemann Nielsen & Hansen 1959, Cole & Cloern 1984) of P_m^B . This measure of respiration has also been shown to vary with species composition (range of 5 to 50% of P_m^B ; Langdon 1993 and references therein) and day length (5 to 13% of P_m^B ; Gilstad et al. 1993). Furthermore, due to the nature of ^{14}C measurements and to authors' methodologies and assumptions, it is often unclear whether published measurements of productivity are more nearly net or gross, and occasionally it is difficult to determine whether their measurements are daytime or daily (24 h), or integrated or instantaneous production rates. In a regression for LIS, R_c was equivalent to 0.1% of P_m^B and statistically explained ~8% of the variance in P_m^B . Therefore our data do not support the use of a % P_m^B as a proxy for community or algal respiration.

Mid and bottom waters

Our rates of community respiration in mid and bottom waters during periods leading to and during hypoxic conditions in LIS suggest that water column respiration is primarily responsible for the decrease in bottom water oxygen concentrations observed in LIS during summer. Measured rates of benthic respiration in the western end of LIS by Mackin et al. (1991) during the period leading up to an hypoxic event were $46.9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in early summer and $15.6 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in late summer. Our summer rates of pelagic respiration near bottom averaged $20.2 \pm 19.8 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (equivalent to $0.84 \pm 0.82 \text{ mmol O}_2 \text{ m}^{-3} \text{ h}^{-1}$). In a 1 m water layer, these values are 50 to 100% of the values of benthic metabolism reported by Mackin et al. (1991). More realistically, if we apply our seasonal ranges in pelagic respiration to a 10 m

depth of water column, which is an underestimate of the depth of the lower portion of the water column during periods of high stratification, the average rate of pelagic respiration measurements in the lower water column during the period leading up to hypoxic events of LIS in the present study ($201.7 \pm 197.9 \text{ mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$) is 5 to 13 times the benthic demand. This relative comparison concurs with Torgersen et al.'s (1997) estimates of the number of days it would take water column processes to deplete a 10 m bottom layer depth with an initial concentration of $220 \text{ mmol O}_2 \text{ m}^{-3}$ (16 to 39 d) versus that of the sediment oxygen consumption processes (55 to 145 d) in spring and summer.

CONCLUSION

We report extensive data showing the temporal and spatial variation of O_2 -based measurements of P - I parameters (α^B , P_m^B), plankton community respiration (R_c), and phytoplankton biomass (chl). The interplay of these biological variables with environmental variables has improved our understanding of the processes primarily responsible for oxygen production and consumption in LIS. Irradiance and water column structure play major roles in the seasonal variability of biomass and P - I parameters (light-adapted state) of phytoplankton. Phytoplankton biomass itself also served as an important indicator for the seasonal changes in P_m^B . Temperature was not a good predictor for production in LIS. Since the knowledge of photosynthetic parameters (P_m^B and α^B) allows us to determine rates of specific-productivity, these results provide empirical support for the statistical use of chl, I_0 and the underwater light field as predictors for rates of gross community production in LIS.

To determine rates of net primary production, however, an estimate of algal respiration is necessary. The relationship between community respiration rates and phytoplankton biomass provides an upper limit to algal respiration, an estimate of algal-related respiration rather than algal respiration alone. Although this relationship is theoretically more robust and more rational than the previously utilized relationship estimate for algal respiration based on a percentage of P_m^B , it is likely to overestimate algal respiration because it includes algal-related respiration of microorganisms. This algal-related respiration accounts for 43 to 60% of the daytime plankton community respiration in the surface waters of LIS. While we believe this result to be accurate, some way in which to specify algal respiration is needed, perhaps one that assumes a basal rate plus a fraction associated with specific productivity (e.g. Langdon 1993). It is not possible to parameterize such a scheme from our data or from ^{14}C measure-

ments of photosynthesis. In any case, given an upper constraint for algal respiration, we feel more confident applying this to our direct, O₂-based rates of gross community production to estimate primary productivity or rates of phytoplankton growth, than is possible with ¹⁴C-based rates of production.

Measurements of plankton community respiration in mid and bottom waters along the main axis of LIS exceed past measurements of sediment oxygen consumption rates in western LIS during periods leading up to and during hypoxic conditions. The magnitude and spatial distribution in these high rates of pelagic oxygen consumption of bottom waters in LIS suggest that these water column processes are likely to be more important than benthic demand in determining the gradient in the oxygen concentrations and hypoxia observed in the bottom waters of LIS.

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