

Drivers of Plankton Patch Formation, Persistence and Decline in East Sound, Orcas Island, Washington

Susanne Menden-Deuer
Assistant Professor of Oceanography
University of Rhode Island
Graduate School of Oceanography
South Ferry Road, Bay Campus
Narragansett, RI 02882

phone: (401) 874-6608 fax (401) 874-6728 email: smenden@gso.uri.edu

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LONG-TERM GOALS

Localized concentrations of plankton (i.e. patches) alter the optical and acoustical properties of the water column and can have significant ramifications for the ecological dynamics of marine communities. The goal of this research is to develop a mechanistic understanding and predictive capability of the *relative* importance of biological versus physical processes in the formation, persistence, and decline of plankton patches. This goal is addressed by concurrent characterization of physical water column structure, advective fluid flow, and plankton population rates of growth and grazing.

OBJECTIVES

The objective of the funded work is to quantify the relative importance of advection and ecological processes to plankton patch formation in the coastal ocean. These objectives will be addressed by simultaneously quantifying (1) spatial and temporal characteristics of large plankton patches (2) fluid flow associated with the patches using Lagrangian drifters, and (3) the plankton population dynamics through simultaneous measurements of phytoplankton growth and mortality rates as measured by changes in Chl a.

APPROACH

The methodological approach of this research is to combine high-resolution analysis of in-situ plankton distributions and the chemical, physical and biological conditions they occur in with laboratory-based measurements of plankton abundance, productivity, and grazer-induced mortality rates. Upon discovery, plankton patches are seeded with Lagrangian drifters and revisited at daily intervals to track the horizontal position of patches and quantify the rates of advection. This research utilizes methods widely used in biological oceanography as well as more recent approaches established and tested during my work in East Sound. Some of the results have recently been published (Menden-Deuer et al. 2010, Menden-Deuer & Fredrickson, 2010) or are in review (Menden-Deuer, in review).

Small boat surveys, East Sound, Orcas Island

East Sound is a temperate fjord within the San Juan Archipelago in the Northeastern Pacific (N 48° 39', W 122° 53', Fig. 1). The fjord has a north-south extent of approximately 9 km, an east-west width of 1 - 2 km and a mean depth of 30 m. Circulation and water-mass exchange with the tidally well-mixed water in Harney channel to the south is restricted by a partial sill at the southwestern terminus of the fjord. Previous, ONR funded work, has established East Sound, Washington as a site of recurring plankton layer presence and provided great insight into the physical forcing mechanisms (Deksheniaks et al. 2001). The presence of distinct plankton layers was subsequently confirmed in a variety of coastal environments, highlighting that layers are a common rather than rare occurrence (McManus et al. 2003). The work described here builds on those results as well as work on the biological composition and dynamics of plankton layers (Alldrege et al. 2000, Rines et al. 2002, Menden-Deuer 2008).

From our land base at the Shannon Point Marine Center, Western Washington University, East Sound is easily accessible by boat within 30 - 45 minutes. Previous work has established that plankton layers in East Sound are continuous and coherent structures on a daily basis, but that significant changes in the composition occur on the order of a few days (Menden-Deuer, 2008). The goal of the 2011 sampling season was to provide a high-resolution distribution of layers within their physical context and measured concurrently to deployment of Lagrangian surface drifters (Fig. 2).

Six transects with 3 to 7 stations at 0.2 nm intervals were located along the main, north-south axis of the sound. A reference station was located outside the sound, where no layers have been observed prior to 2009 (Fig. 1). The goal of this sampling scheme was to increase spatial resolution and determine the edge of layer extent. Layer presence was determined by profiling the water column with a SeaBird 19+ CTD (T, S, P, σ_t) and auxiliary fluorometer (Wetlabs WetStar). Water samples from within PRLs and surrounding waters were collected with a 2L and 10L horizontally mounted Niskin bottle.

Estimates of patch advection

Using drifters (Pacific Gyre SVP) with tethers at 5, 10, or 15 m depth, water parcels were tracked in a horizontally Lagrangian but vertically restricted manner. Drifters report position via a GPS enabled satellite-modem surface buoy attached to a subsurface drogue. In the field, tracking the position of plankton patches while taking repeated vertical profiles of water column properties allowed us to estimate both the lateral advection of patches and the change in patch structure in the same parcel of water. Drifter depth and deployment location were determined both based on instantaneous measurements of vertical water column properties, mainly the fluorescence profile and the horizontal gradients in patch structure within the entirety of the sound.

Biological characteristics and rate measurements

Previous years calibrations have shown that the WetLabs WetStar fluorometer agrees reasonably well with Chl a measurements extracted from whole water samples. Thus, in 2011, no direct Chl a measurements were made. Whole water samples were directly analyzed for species composition on an inverted microscope and if needed, preserved with Lugol's iodine to a final concentration of 2% (Menden-Deuer et al. 2001) for taxonomic analysis. These measurements help place the field and rate measurement data in a quantitative, biological context. To establish the rates of change of plankton abundance three different methods are used in the course of this field work: two independent methods to measure primary productivity, and the dilution method to measure zooplankton grazing impact. In

combination, these methods quantify both the potential for plankton layer occurrence as well as dissipation due to biological processes.

The rate of change in phytoplankton biomass is measured using the radiolabeling method that was first developed by Steemann Nielsen (1952) to quantify photosynthesis. Since its invention, the method has been effectively applied to measure phototrophic processes, including phytoplankton growth rates, carbon to Chl *a* ratios (Welschmeyer & Lorenzen 1984), heterotrophic protist grazing rates (Montagnes & Lessard 1999), and cellular carbon content (Putt & Stoecker 1989, Crawford & Stoecker 1996). The radiolabeling technique exploits the fact that photosynthetic organisms incorporate inorganic CO₂ to generate their tissue, and measurements with a scintillation counter are sensitive enough to detect ¹⁴CO₂ within a single cell (e.g. Menden-Deuer & Lessard 2000). A known fraction of the total CO₂ is offered as a radiolabeled tracer (¹⁴CO₂). The uptake rate of the tracer can then be used to calculate photosynthetic rates.

Primary productivity experiments were conducted in a controlled light box, with positions that correspond to known light levels. This allowed the establishment of photosynthesis rate vs. irradiance curves (PE curves) and calculation of photosynthesis parameters, including maximum rate and half saturation constant. In these experiments, 14 light levels were used to estimate the rate of photosynthetic activity and capacity. The advantage of this experimental approach is the much greater replication as well as estimation of photosynthetic potential.

The dilution method (Landry and Hassett 1982) is used to complete the assessment of biological processes that alter plankton standing stock and productivity. Specifically, it was used to assess potential loss of phytoplankton due to grazing mortality and subsequent increases in zooplankton due to growth. The dilution experiments were conducted according to protocols established by Suzanne Strom (WWU) and her laboratory. Whole water samples were prescreened through a 200 μm mesh, so that larger zooplankton were eliminated from the experiments, to avoid grazing of copepods on the microzooplankton predators. Two dilution levels (5 and 100%) were run in triplicate. Some experiments had an additional nutrient-addition treatment to avoid nutrient limitation of the primary producers. All samples were incubated for 24 hrs, cooled with ambient seawater, and exposed to ambient surface light levels. Light levels were adjusted to the sample depth with neutral density screen.

This work builds upon prior ONR funded work in East Sound conducted by (incomplete, in alphabetical order) Alldredge, Cowles, Donaghay, Grünbaum, Holliday, McManus, Perry, and Zaneveld.

WORK COMPLETED

In 2011, field work was conducted between July 17th and August 2nd 2011. A total of 11 day cruises to East Sound, Orcas Island, were undertaken from the land base of Shannon Point Marine Center, Anacortes, Washington. During a typical cruise, a total of 31 stations were visited comprising five longitudinal transects of the sound and one transect outside of the sound (Fig 1). At each station high resolution (5-10 cm) vertical profiles of the physical (temperature, salinity and light intensity), chemical (dissolved oxygen), optical (beam transmission), and biological (phytoplankton fluorescence) properties of the water column were recorded with a SeaBird CTD 19+.

Discovery of layer presence and distribution was possible through real time acquisition of fluorescence data. The CTD mounted fluorometer has been calibrated for taxonomically different plankton

communities in East Sound for 5 years now and is considered a reliable indicator of phytoplankton biomass. In 2011, water parcel movement was tracked using three Pacific Gyre SVP Lagrangian drifters sampling position via GPS at least every 10 minutes. Drifters tracked water movement at a depth of 5 m. On each cruise day, two to three drifters were deployed continuously for up to two days before retrieval and redeployment. A cumulative total of 440 hours of drifter tracks with a median deployment of 24 hours were recorded during 22 deployments of three drifters. In addition, a manuscript on the photosynthetic rate measurements and their relation to layer formation potential was completed and is currently in review.

RESULTS

Phytoplankton biomass was generally low in July/August 2011 at $< 10 \mu\text{g Chl a l}^{-1}$ (estimated). Nonetheless, presence of several layers and their disappearance was observed (Fig. 3). The biomass was dominated by the large diatom species *Rhizosolenia cf. pungens*, *Leptocylindrus minimus*, *Cerataulina pelagica*, and *Coscinodiscus* spp. Intense surface layers of the heterotrophic dinoflagellate *Noctiluca scintillans* were also observed. The community composition remained diverse and very similar throughout the observation period, and large diatoms dominated the biomass, unlike previous years when rapid shifts in community composition typically dominated by 1 to 2 species were observed. By and large, we were observing the same population for the entirety of the period.

Since all of the phytoplankton species are non-motile, with the exception of buoyancy control for vertical motion, tracking layer distribution via Lagrangian drifters is a good approximation. The surface drifters revealed a highly dynamic picture of significant water exchange with waters outside the sound (Fig. 4). However, more quiescent periods were also recorded. The drifter deployments revealed that plankton patches in the north are subject to much lower horizontal advection than in the southern sound. For most deployments, water in the upper basin stayed within the upper basin during drifter observation, either rotating around the edge of the basin or oscillating slightly along sound. Drifters deployed at the lower sound moved primarily linearly along sound. On one occasion, 26th of July 2011, a drifter deployed at the south end of the fjord was recovered ~3 miles southward, indicating significant export of water from the sound (Fig. 5). The latter may also indicate contribution of biomass generated within East Sound to areas outside. It is noteworthy that during the same tidal cycle, flow in the northern part of the fjord was much more restricted. A quantitative analysis relating water motion to layer dynamics is underway.

Based on samples collected in prior seasons, I completed an analysis of the layer associated primary production rates (Menden-Deuer, in review). The following results are based on that analysis. A question driving this research was to identify if phytoplankton associated with plankton patches were characterized by intrinsically higher photosynthetic capacity or performance. Two analyses were conducted to determine if the P vs. E parameters of layer samples indicated higher photosynthetic potential for those phytoplankton communities. First, I compared if the P vs. E parameters of layer samples were overall distinguishable from samples collected at stations that did not have a structured phytoplankton distribution - hereafter referred to as non-layer samples - as well as from samples collected at stations with distinct phytoplankton layers but below or above those layers - hereafter referred to as outside layer samples. There were a total of 94 samples: 48 non-layer, 32 inside, and 14 outside layer samples. This analysis showed that none of the P vs. E coefficients for layer samples were significantly different from outside and non-layer sample P vs. E coefficients (Fig. 6). This indicates that phytoplankton communities from inside plankton layers were not inherently distinguishable by an overall higher photosynthetic potential or capacity.

Second, P vs. E parameters for a subset of samples collected at the same station and date at different depths inside and outside layers were compared specifically with one another. There were 28 samples, 14 each from inside and outside layers. In this direct comparison, samples from inside layers did have significantly higher photosynthetic potential, with significantly higher P_{\max} ($p=0.01$) and α ($p=0.03$) values (Fig. 7, Table 4). Although the K_s value was lower for samples from within layers, the difference was not statistically significant ($p=0.81$). Therefore, samples captured inside a layer at a particular station showed higher photosynthetic potential than samples captured either above or below (outside) layers. These results indicate that within a specific water column, phytoplankton captured inside plankton layers had a localized higher photosynthetic potential than phytoplankton sampled from elsewhere in the water column. However, because these samples were taken in the field, according to the conditions found, rather than a laboratory experiment, there was a confounding effect in that layer samples occurred at significantly shallower depth, 4 m shallower on average than non layer samples. Therefore, the higher photosynthetic potential may reflect a localized acclimation to higher incident light levels at shallower depth rather than an intrinsic difference in photosynthetic potential of layer-associated phytoplankton.

Volume specific productivity rates, normalized to Chl *a* were calculated to determine the effect of primary production on layer development, persistence and decline. The subset of experiments where P vs. E curves were available from both in and outside layers at the same station were used for this comparison ($n=28$). Primary production inside layers was significantly higher than outside of layers (Fig. 8, $p<0.001$). This result was independent of whether *in-situ* or averaged over the day light levels were used to calculate productivity. Median in layer production rate was nearly 2-fold higher at $1.93 \text{ mg C mg Chl a hr}^{-1}$ inside layers and $1.03 \text{ mg C mg Chl a hr}^{-1}$ outside layers, based on instantaneous PAR measured at time of sample capture. Using an hourly averaged maximum PAR from the sampling date, adjusted to sampling depth using the profile specific attenuation coefficient, yielded inside- and outside-layer production rates of 2.97 and $1.52 \text{ mg Chl a hr}^{-1}$ respectively. The average in layer sampling depth was 2.3 m ($\pm 1.2 \text{ m}$) and the median outside sampling depth was 6.7 m ($\pm 3.2 \text{ m}$). The higher production rates may have been due to the often shallower depths, including surface, at which layers formed and thus received higher irradiance levels. Comparison of the *in-situ* irradiance at time of sampling with the P vs. E derived half saturation constant showed that about 60% of the samples were exposed to irradiance levels at or above the half saturation constant (Fig. 9). Layer samples were captured both above and below half saturation irradiance levels.

IMPACT/APPLICATIONS

This work characterizes the dynamics of biological patch formation and dissipation with high spatial and temporal resolution. Our explicit goal is to quantify the relative importance of biological rates of growth and grazing versus physical advection on the formation, persistence and decline of plankton patches. We have been able to quantify the rates of phytoplankton growth and predator induced mortality within the physical, chemical and biological conditions they occur in. Our results show that plankton rich layers and patches are sites of rapid growth and nutrient uptake. Moreover, there is significant predation within patches that limits accumulation of biomass. Essential are the availability of nutrients that are supplied only by tidally induced replacement of water masses. My working hypothesis is that this interplay of biological, physical and chemical drivers provides temporally varying drivers of plankton patch formation, maintenance and decline. These results provide essential data for empirically motivated models that predict the time rates of change of plankton patch intensity and size, and the resultant changes in the optical and acoustical properties of the water column.

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PUBLICATIONS AND PRESENTATIONS

Publications

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FIGURES

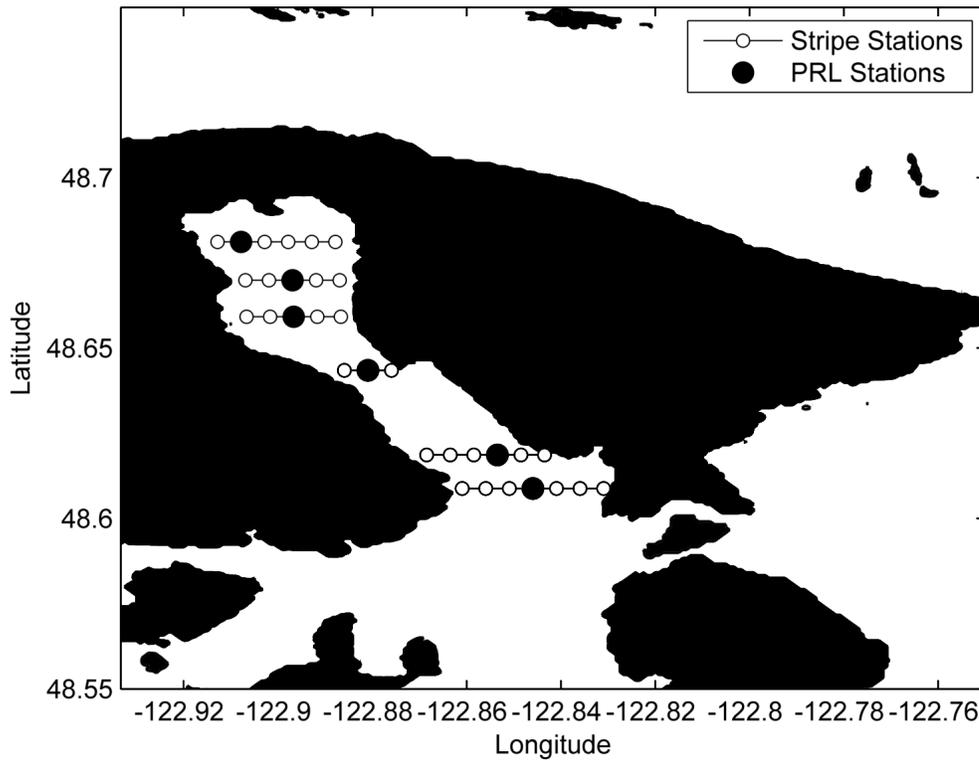


Figure 1 Approximate station locations of 31 sampling sites aligned along 6 horizontal transects in East Sound, Orcas Island, WA. Main stations are shown as filled circles. Stations were located approximately 0.2 nautical miles distance. Transects were placed to produce high-resolution layer maps in the north end and contrast those with the southern end of the fjord.



Figure 2 Surface drifter (SVP Microstar, <http://www.pacificgyre.com>) just after deployment at Station 5 on August 2nd 2011. Black drogue is still visible at the surface. The orange surface sphere contains a GPS unit that is remotely tracked and provides position information at 10 minute intervals.

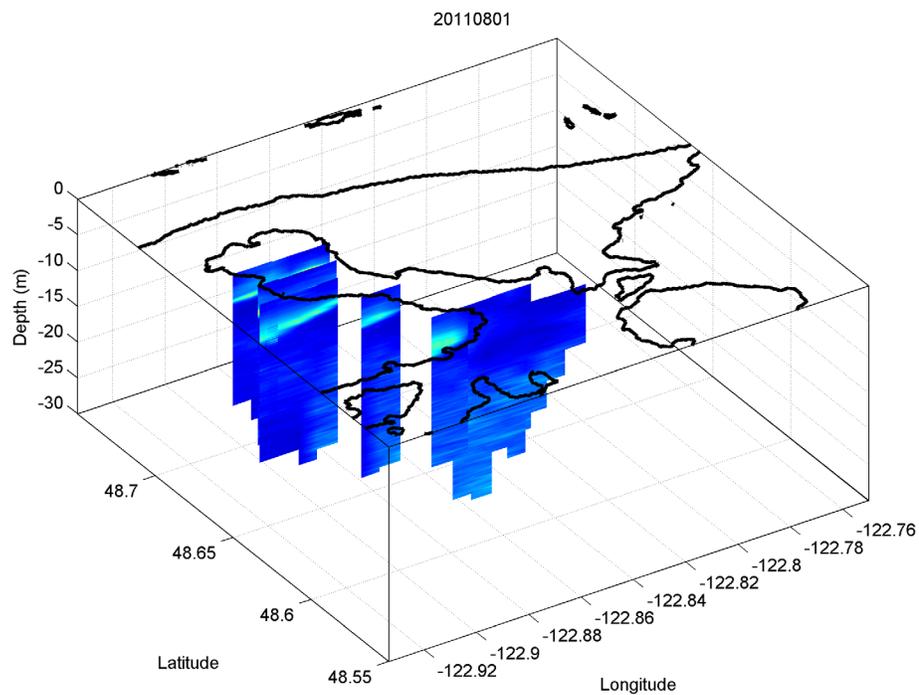
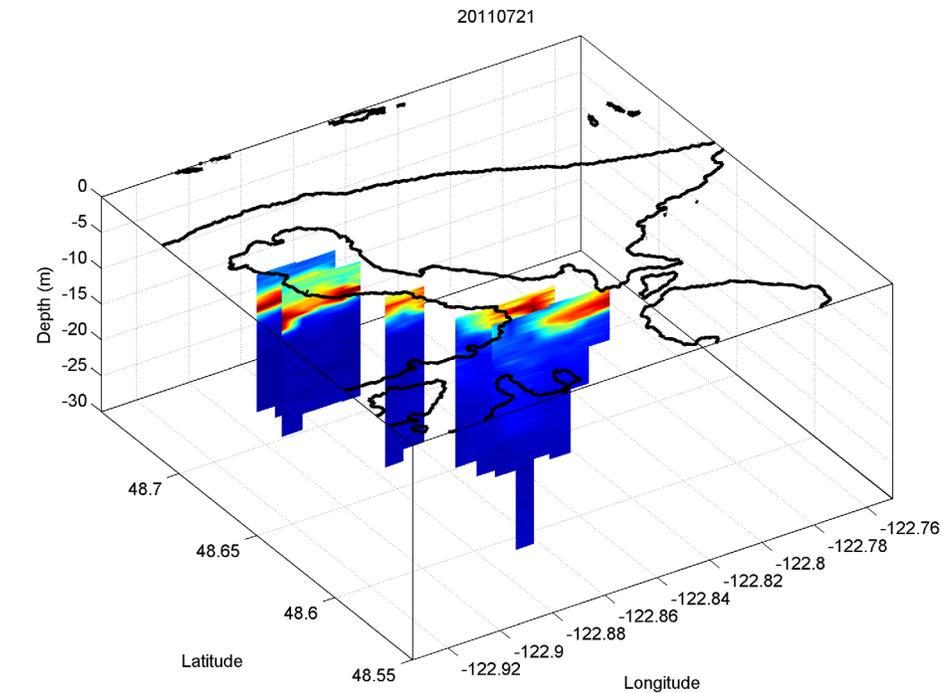


Figure 3 Distribution of Chl a induced fluorescence in East Sound, Orcas Island on July 21st 2011(top) and August 1st 2011 (bottom). Fluorescence is proportional to color, with warm colors indicating higher values; reds correspond to $\sim 10 \mu\text{g Chl a l}^{-1}$. Both plots are on the same fluorescence scale bar. While intense layers were observed on July 21 2011, nearly all phytoplankton had disappeared from the water column by August 1st 2011.

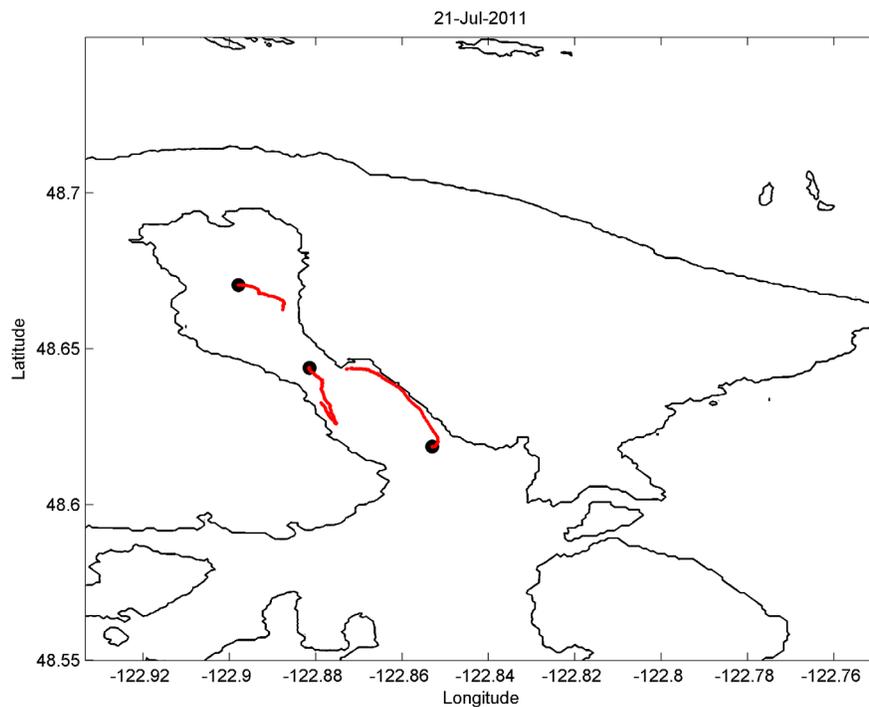
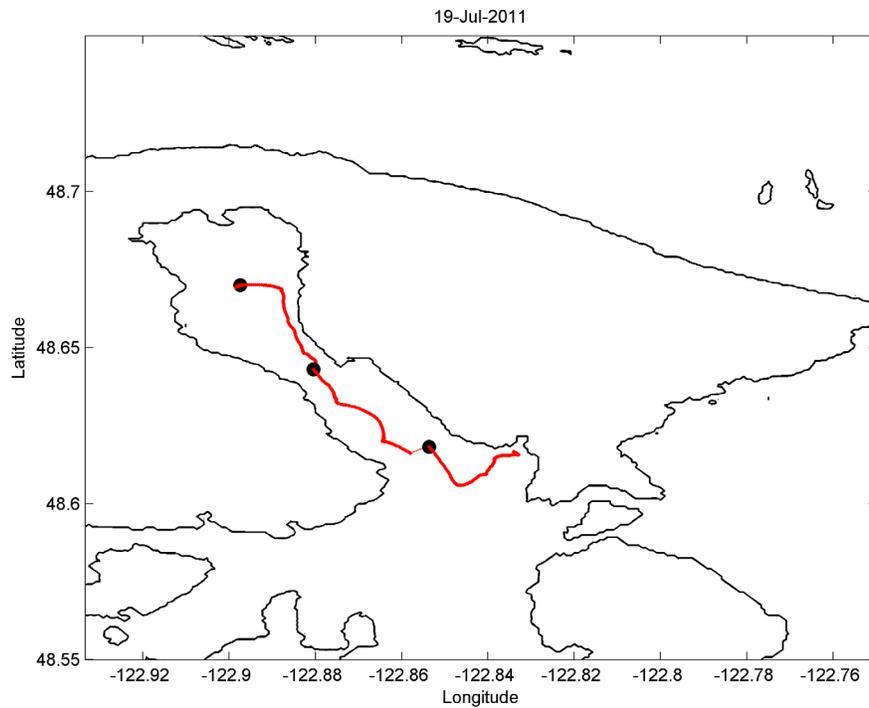


Figure 4 Drifter tracks during 24 hr deployments on 19th and 21st of July 2011. Black indicates initial drifter deployment location and red line is the composite track based on positions recorded at 10 minute intervals. Drifters were deployed for a complete tidal cycle and distance between beginning and end positions indicate net water motion.

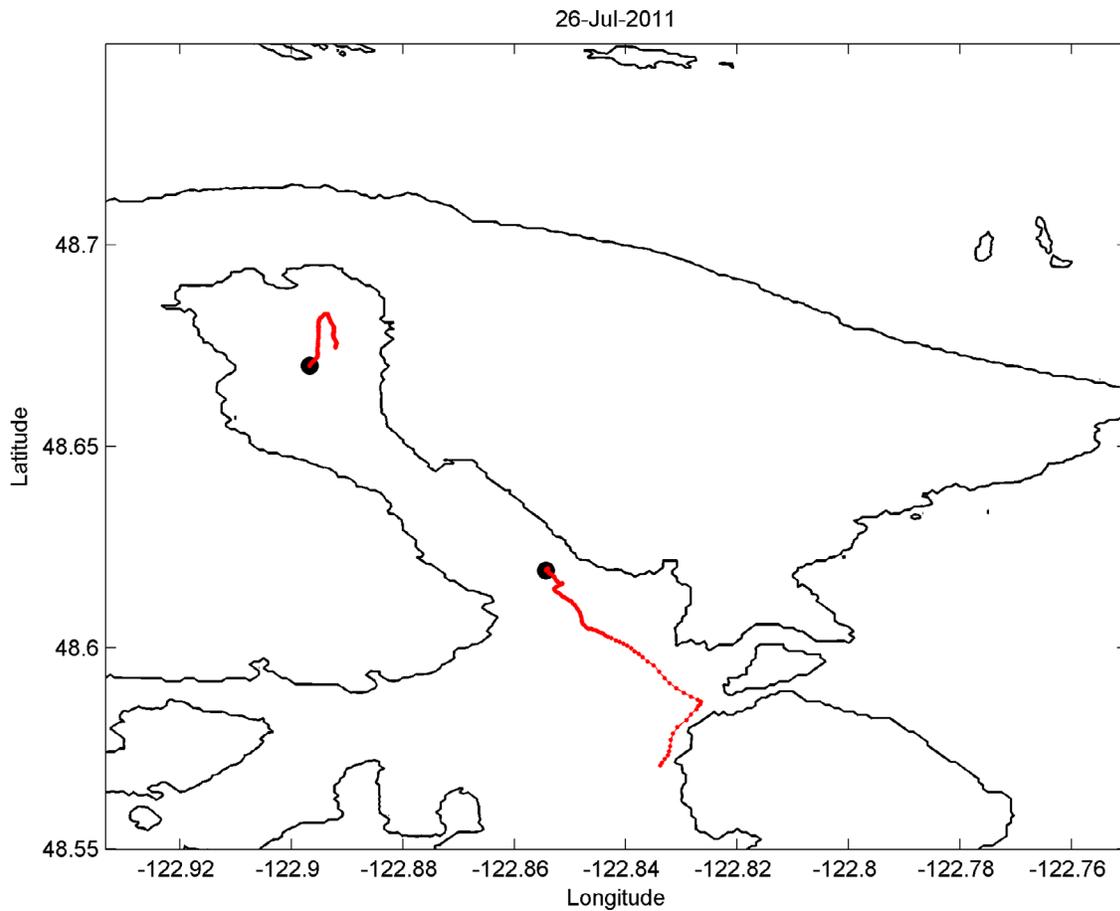


Figure 5 Drifter track during 24 hr deployments on 26th of July 2011. Black indicates initial drifter deployment location and red line is the composite track based on positions recorded at 10 minute intervals. Drifters were deployed for a complete tidal cycle and indicate net water motion. The net distance traveled for the southern drifter is approximately 3 nautical miles. Note the difference in advection between the northern and southern drifter during the same tidal cycle.

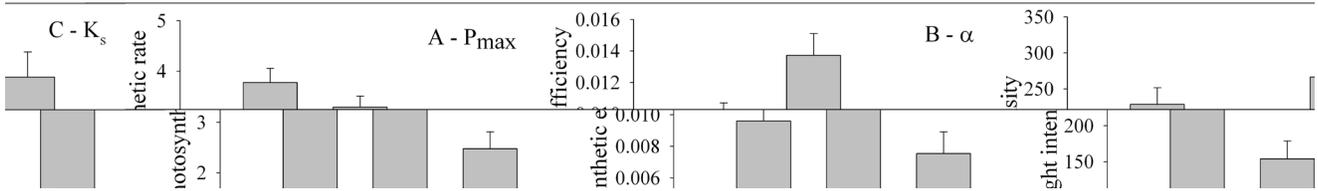


Figure 6 Median P vs. E coefficients for phytoplankton communities drawn from within plankton layers ($n=32$) compared to samples taken at the same station, outside layers ($n=14$) and at stations without distinct plankton layers ($n=48$). Error bars are one standard error of the mean. Units are omitted from y-axis labels and are:

P_{max} [$mg\ C\ mgChla^{-1}\ hr^{-1}$], α [$mg\ C\ mgChla^{-1}\ hr^{-1}$ ($\mu mol\ photons\ m^{-2}\ s^{-1}$) and K_s [$\mu mol\ photons\ m^{-2}\ s^{-1}$] respectively. Layer associated plankton communities had higher photosynthetic potential, due to higher α , and lower K_s values than non-layer and outside samples, but these differences were not statistically significant from non-layer and outside layer samples

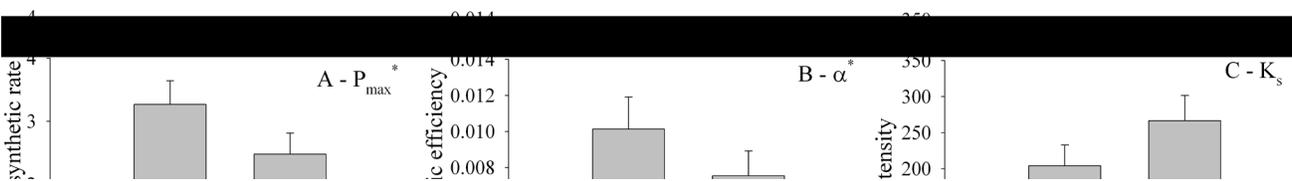


Figure 7 Contrast of median P vs. E coefficients for phytoplankton communities drawn from inside plankton layers ($n=14$) and outside, at a depth 2m above or below the layer ($n=14$). Errorbars are one standard error of the mean. Layer samples had significantly higher maximum photosynthetic rates ($p=0.01$) and photosynthetic efficiencies ($p=0.03$) but no difference was observed for the half saturation constant ($p=0.81$). Layer samples were taken at significantly shallower depth, which may have led to localized acclimation to higher incident irradiances.

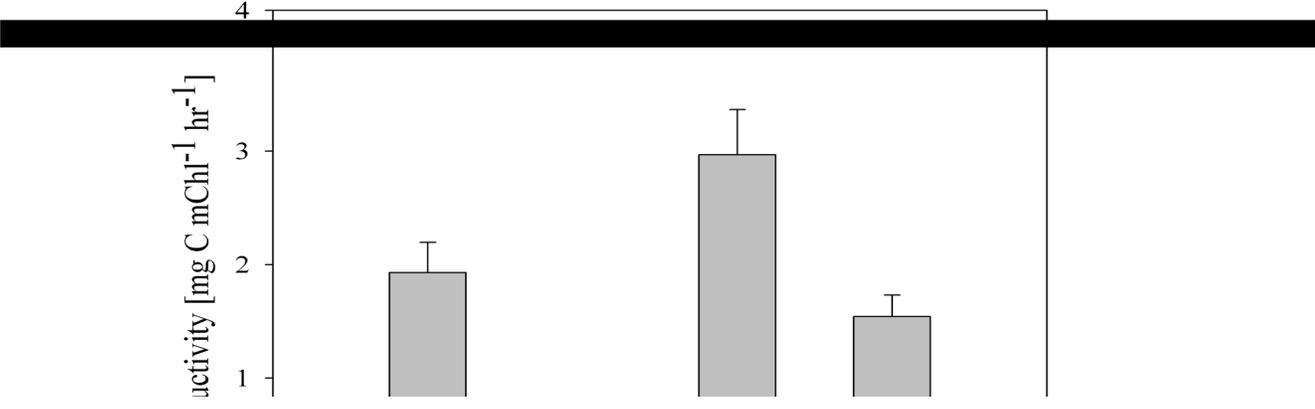
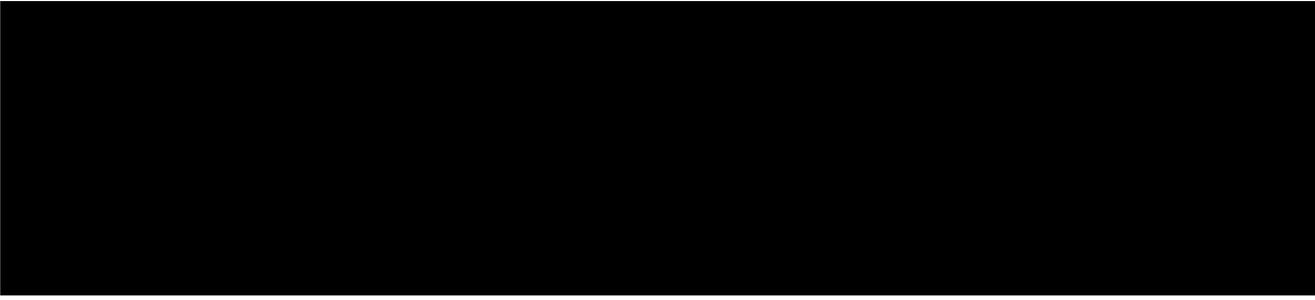


Figure 8 Median volume specific productivity rates (mg C mg Chl⁻¹ hr⁻¹) for samples collected inside and outside layers (n=28). Production was higher inside layers (p<0.001) irrespective of whether light levels were based on in-situ irradiance or averaged, depth adjusted irradiance from surface measurements. The difference was due to the shallow layer depth and not due to systematic differences in photosynthetic capacity of layer associated phytoplankton communities.

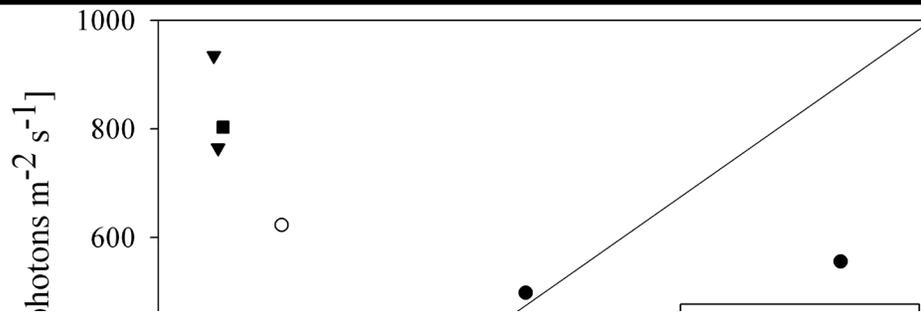


Figure 9 Half-saturation constants measured from laboratory P vs. E incubations relative to PAR measured in-situ at sampling depths. Samples are distinguished by season and whether samples were captured inside (open symbols) or outside of layers (closed symbols). The black line indicates the 1:1 relationship. Samples taken at PAR irradiance levels exceeding K_s shown above the 1:1 line, samples taken at irradiance levels below K_s shown below the 1:1 line. 60% of the plankton communities were sampled at PAR levels equal to or greater than the half-saturation constant. Samples taken within layers were not conspicuous among the set.