

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

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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 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 environmental and ecological processes to plankton patch formation in the coastal ocean. These objectives are 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 and (4) statistical analysis of environmental and biological factors associated with phytoplankton patch presence and intensity.

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.

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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 (Dekshenieks 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). Each field season used progressively higher spatial resolution of sampling stations, optimizing the in a tradeoff between water collection for rate measurements (lower spatial resolution) and high resolution assessment of in situ dynamics (fewer rate measurements). 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.

Prediction of plankton patchiness

Here, our goal was to develop an empirically-based predictive algorithm that would enable the prediction of plankton patchiness based on a range of autonomously acquirable water column characteristics. We used a large data set of water column profiles collected over 3 years in a shallow fjord that included both PRL and non-PRL samples to determine if we could 1) identify a unique set of parameters to predict the presence of PRL samples and 2) provide an estimation of patch strength. We found that patch presence may be predicted from water column stability parameters and that patch intensity can be estimated using a complex combination of passively measured variables including depth, temperature, salinity, PAR, beam transmission, and fluorescence.

Statistical analyses were performed using Matlab and included regressions of measured and calculated variables, principal component analyses (PCA), and comparisons of physical parameter distributions for patch and non-patch samples using a two sample Kolmogorov-Smirnov test. Type II linear regressions were performed for the analysis of in-situ variables as these were measured with error. Multiple generalized additive models (GAMS) (Hastie & Tibshirani 1986), i.e. linear models composed of a sum contribution of multiple variables, were created to test if the patch intensity (PI) of any given sample could be estimated from 1) a combination of the variables measured by the CTD package (depth, temperature, salinity, PAR, beam attenuation) and with and without fluorescence or from 2) the variables measured by the CTD package plus the calculated parameters relating to physical

properties of the water column (Brunt-Väisälä frequency, Thorpe scale, and turbulent dissipation rate). The GAMs were created in R (R64.app for Mac OS X GUI 1.36 (5691 Leopard build 64-bit, www.r-project.org).

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

A field season was conducted annually between 2008-2011, lasting between 3-6 weeks each and combining laboratory and field work. Field work comprised day cruises from our land base Shannon Point Marine Center, Anacortes, Washington to East Sound, Orcas Island. During a typical cruise, a total of at least 5 and up to 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.

Analysis of in situ measurements were completed during the field season, whereas concentrations and rate measurements were analyzed in the subsequent time period. Manuscripts have been published continuously, see below. There are 2 remaining manuscripts. The first describing an empirically based algorithm for layer detection, which will be submitted within the next 1-2 months. Another manuscript relating to the drifter data is in prep.

RESULTS

The results presented here are in addition to results presented in prior years annual reports and peer reviewed publications resulting from the ONR support. In brief summary, we were able to accomplish the research proposed and exceeded the goals in some instances. Highlights from the results are as follows:

1. Phytoplankton patches are trophic hot spots: Protistan grazing (copepods excluded) on phytoplankton patches was >2 fold higher within patchy structures (see Menden-Deuer & Fredrickson 2010).
2. Phytoplankton patches are demographic hot spots: Phytoplankton within patches are physiologically acclimated to have higher photosynthetic yield than non-patch phytoplankton (see Menden-Deuer *in press*).

3. Phytoplankton patches are production hot spots: Patches contributed the majority of depth integrated water column primary production despite only occupying ~12% of the water column (see Menden-Deuer & Fredrickson 2010).
4. Nutrient concentrations suggest water masses associated with patches were isolated for several days and do not exchange with waters at other depths (see Menden-Deuer *in press*).
5. Fluorescence alone was an insufficient predictor of PRLs, due in part to the possible influence of non-photochemical quenching (NPQ) in surface waters.
6. Break down of grazing pressure can lead to rapid patch formation (<48 hrs) (see Menden-Deuer et al. 2010).
7. Environmental conditions can either directly (temperature) or indirectly (species composition) drive grazing pressure (see Lawrence & Menden-Deuer 2012).
8. A predictive algorithm could identify patch presence with 70-100% accuracy as a function of water column stability but patch intensity parameters could only be identified with 30% accuracy (Fig. 2, see Graff & Menden-Deuer *in prep.*).
9. Patches form due to an interplay of the conditions and communities outside and inside patches (Fig. 3, see Menden-Deuer & Fredrickson, 2010, Menden-Deuer *in press*).

IMPACT/APPLICATIONS

This work characterizes the dynamics of biological patch formation and dissipation with high spatial and temporal resolution. Our explicit goal was 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 provide novel insights, documenting for the first time to my knowledge that patches are indeed trophic hotspots. This is the first empirical documentation of a frequently a longstanding hypothesis. The importance of documenting the importance of patchiness for rate measurements empirically is that we provide a quantitative documentation that average analyses of biological processes in the coastal ocean will lead to false predictions. Inaccuracies arise because the non-linear dynamics, particularly of exponentially growing phytoplankton can not be reproduced based on mean field estimates. Through the support rendered by ONR, we have been able to document that plankton rich layers are sites of rapid growth and nutrient uptake. Moreover, there is significant predation within patches that limits accumulation of biomass. At this particular field site, it is essential that nutrients are supplied only by tidally induced replacement of water masses, making instability, which is counterproductive to patch formation and persistence a prerequisite of patch longevity. My working hypothesis is that this interplay of biological, physical and chemical processes provides temporally varying drivers of plankton patch formation, maintenance and decline. Our work has shown that understanding plankton patchiness is an important topic for understanding and quantifying phytoplankton abundance, distribution, and production as well as food web and biogeochemical ramifications. These results provide essential data for 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. Together these data deliver a predictive frame work for the formation, persistence and decline of plankton patchiness and the resultant effects on water column properties.

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PUBLICATIONS AND PRESENTATIONS

Publications

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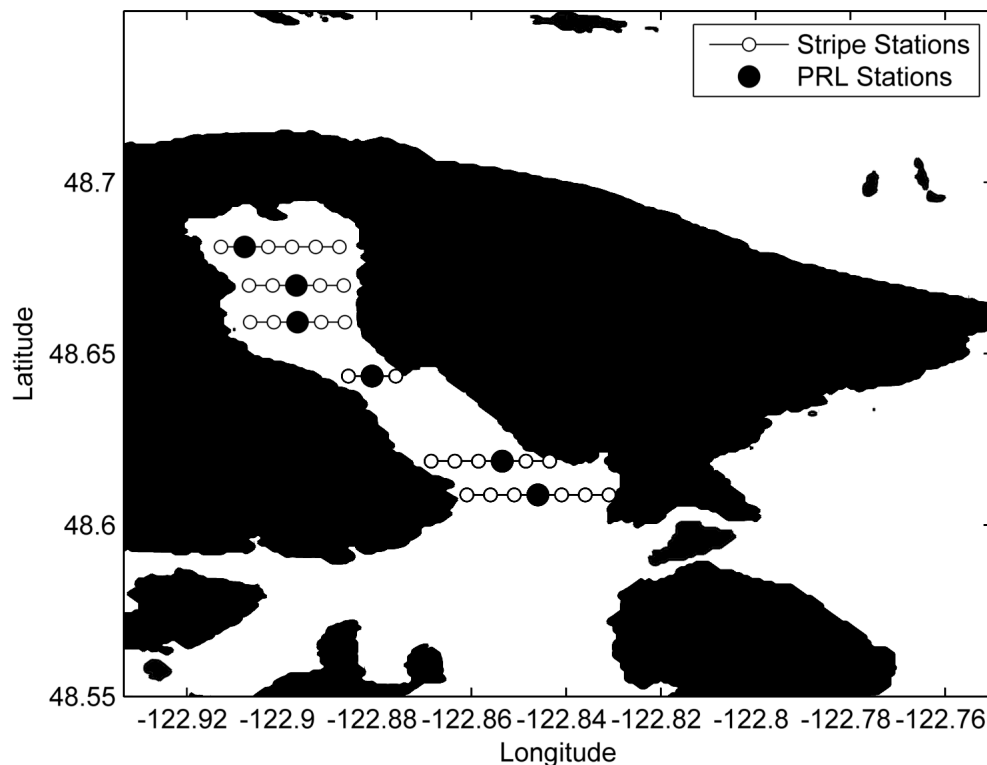


Figure 1 Station locations of 31 sampling sites aligned along 6 horizontal transects in East Sound, Orcas Island, WA. Main stations are shown as filled circles. Stations were located approximately 0.2 nautical miles distance. Transects were sited to produce high-resolution layer maps in the north end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

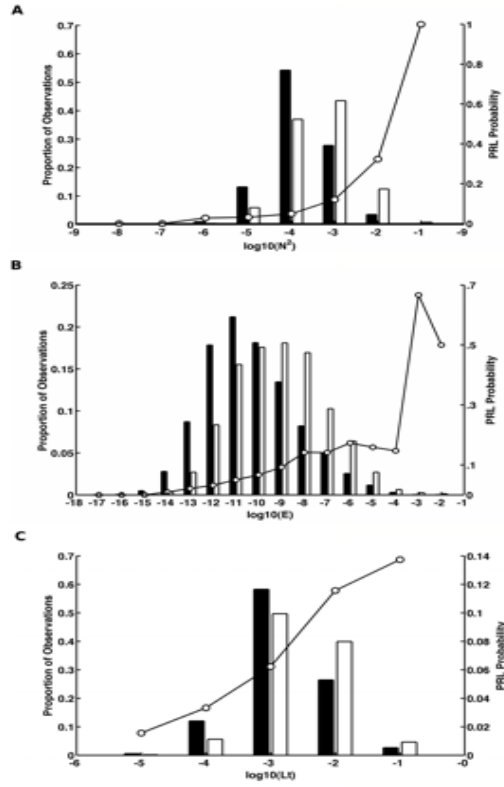


Figure 2 Normalized histograms of A) the Brunt-Väisälä frequency (N^2), B) the turbulent dissipation rate (ϵ), and C) the Thorpe scale (L_t) for all samples (black) and patch samples (white). Probability (circles) of samples occurring within patches increased significantly with increasing water column stability. Patch occurrence can be predicted from water.

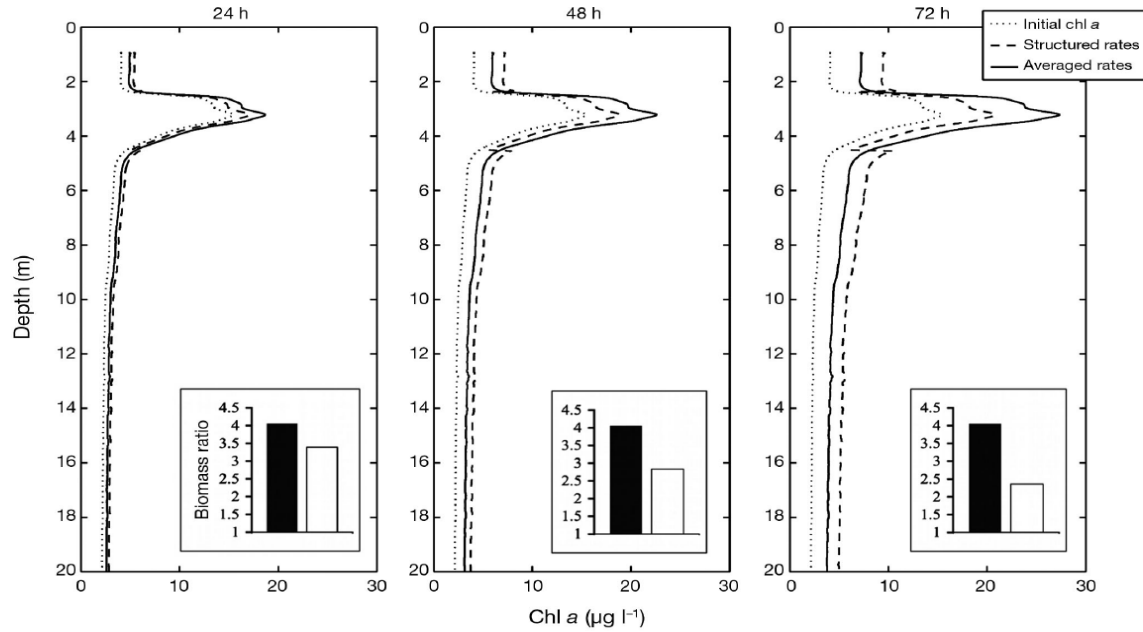


Figure 3 Model predicted development of a phytoplankton layer over 72 hrs assuming averaged vs structure dependent zooplankton grazing and phytoplankton growth rates. Inset shows the ratio of biomass inside vs outside the layer, for the average (black bars) and structured rate models (open bars). Assumption of the empirically observed, structure-dependent grazing rates predicted rapid biomass accumulation outside layers and a decrease in layer intensity over time. These differential biomass accumulation rates lead to patch erosion after 48 h compared to persisting layers assuming uniform and averaged grazing rates. Note reversal of peak biomass accumulation inside and outside of layers depending on whether averaged or structured rates were assumed.