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Spatial and temporal characteristics of plankton-rich layers in a shallow, temperate fjord

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ABSTRACT: Between June and October 2005, a CTD profiler with mounted fluorometer identified the presence and extent of plankton-rich layers (PRLs), i.e. horizontal patches of high plankton concentrations bordered by steep gradients, in East Sound, a shallow fjord in Washington, USA. The suitability of this profiling approach for identifying the meter-scale plankton layers was verified through correlation analysis, which showed that *in situ* fluorescence was significantly correlated with all subsequent proxy measurements of phytoplankton abundance, including extracted chlorophyll *a* concentration and plankton biomass. Species abundance and community composition within and outside the layers were analyzed during peak layer occurrence in July 2005. Layers contained up to an order of magnitude more phytoplankton biomass than surrounding waters. Furthermore, this analysis showed that (1) plankton layers were horizontally coherent, because the species composition of samples from within PRLs from up to 5 stations collected on any given day were statistically indistinguishable; (2) layers were not continuous in time, since species composition changed significantly between sampling days; and (3) layers could have formed within East Sound, since no differences were observed in species composition among samples collected at any depth. Phytoplankton biomass was dominated by the diatom genus *Chaetoceros* (up to 95%), whereas heterotrophic protists (5 to 200 µm) were dominated by thecate dinoflagellates (up to 80% of biomass), with oligotrich ciliates and athecate dinoflagellates at times abundant (up to 40% of biomass). Motile heterotrophic protists were significantly aggregated within phytoplankton prey layers, which confirmed predictions from prior laboratory and modeling work. Biomass of phytoplankton prey species within PRLs uniformly exceeded the dominant predator's survival threshold, whereas prey concentrations outside PRLs would not support growth in all but 3 samples. These observations suggest that PRLs may be biological hot spots where trophic and demographic rates are enhanced and that biological processes could drive plankton layer formation, persistence, and decline.

KEY WORDS: Plankton patches · Spatial ecology · Heterotrophic protists · Food-web dynamics

INTRODUCTION

Phytoplankton distributions in the ocean are frequently heterogeneous in time and space. Knowledge of the spatial and temporal characteristics of patch formation and persistence are essential to predicting their consequences for trophic and demographic dynamics in pelagic food webs and the degree of export production to higher-order consumers. The species composition and population dynamics of plankton patches may hold important cues for identifying processes driving patch formation, persistence, and decline. Intensive efforts and improved instrumentation have revealed highly structured distributions of phytoplankton or their proxy measurements (e.g. fluorescence or extracted chlorophyll *a*, chl *a*) in a range of coastal and oceanic environments (e.g. Cowles 2004, McManus et al. 2005). Often these patches form horizontally extensive, sometimes km-scale layers that persist for several days and contain up to 5 times greater phytoplankton

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or marine snow concentrations than the rest of the water column (Eppley et al. 1968, Kiefer & Lasker 1975, Bjørnsen & Nielsen 1991, Donaghay et al. 1992, Alldredge et al. 2002, Rines et al. 2002, McManus et al. 2003). Such concentrations of particulate organic matter can dramatically affect the acoustical and optical characteristics of the water column (Holliday et al. 2003) as well as the ecological dynamics of planktonic communities. The unifying features emerging from previous studies characterizing phytoplankton layers are their close association with the pycnocline, their limited vertical extent and, in the epipelagic, chl *a* fluorescence signals that exceed background by at least 3-fold (Dekshenieks et al. 2001). The presence of distinct plankton layers has been confirmed in a variety of coastal environments (McManus et al. 2005). Circulation patterns that promote the formation of a stabilizing, physical structure (pycnocline) appear conducive to layer formation, although the shape and association between the biological layer and the chemical or physical structure that surrounds it need not be identical (Cowles 2004). Nonetheless, the strong association between physical and biological structure confirms the fundamental role physical processes play in establishing the environmental conditions necessary to facilitate the formation or maintenance of extensive layers of high plankton concentrations.

Layer boundaries are marked by steep gradients in biological, physical, and chemical properties. These gradients are central to the layer's biological function and importance. Traditional oceanographic methodology averages measurements over vast volumes (e.g. plankton nets), yielding bulk estimates of rates and concentrations. This approach is motivated both by the enormous spatial scales that need to be surveyed and the lack of methodology that would provide high-resolution data on meter-scales or less. Despite these methodological limitations, it has long been suggested that measurements of small-scale heterogeneity would provide information vital to understanding the ecological dynamics of the system. For example, Mullin & Brooks (1976) observed that planktonic predators reproduce at higher rates than would have been predicted based on measured average prey concentrations. Thus, the authors suggested that prey must occur in patches and predators must be able to access these patches to exploit higher prey concentrations. Although highly likely, tests of that hypothesis have been difficult to conduct *in situ*.

Many planktonic predators have mechanical and chemical sensory capacity to perceive ecologically relevant information (e.g. Levandowsky & Kaneta 1987, Jakobsen 2001), which could aid in the exploitation of heterogeneous prey distributions. For many predators, environmental stimuli modulate the individual's swimming behavior and thus ultimately its position in the water column and encounter with the environment. At least under laboratory conditions, protistan predators in a structured water column rapidly aggregated to and remained within isolated prey patches (Menden-Deuer & Grünbaum 2006). We estimated that the concentration of prey in patches would alter predator population dynamics from starvation to growth. Moreover, presence of predator foraging behaviors increased estimates of ingestion and growth rates by over an order of magnitude. Thus, the presence of prey patches, including layers, could significantly alter the trophic and demographic rates of the system, and biological processes could in turn alter the scales of patch persistence and decline.

To determine if prey patches could alter trophic dynamics *in situ*, the present field study attempted to quantify the occurrence of phytoplankton layers in the coastal ocean and to gain insight into their ecological role. Specifically, this study aimed to (1) identify the spatial and temporal scales of layer coherence, extent, and persistence through analysis of plankton community composition, (2) distinguish local from external sources of the layer communities, and (3) quantify the relative distribution of photo- and heterotrophic species to identify the potential role of patches in the food web. The overall goal was to estimate the effect of layers on food web dynamics and investigate the potential for biologically driven changes in layer formation, persistence, and intensity.

MATERIALS AND METHODS

Study site and survey design. East Sound is a temperate fjord within the San Juan Archipelago in the northeastern Pacific (48° 38.61′ N, 122° 52.75′ W). The fjord has a north–south extent of approximately 9 km, an east–west width of 1 to 2 km, and a mean depth of 30 m. Circulation and exchange with the tidally well-mixed water outside are restricted by a partial sill at the southwestern terminus of the fjord. Up to 4 stations, 1 to 2 km distant from each other, spanning the axis of the sound, and 1 additional station just outside East Sound were sampled between June and October 2005 (Fig. 1). Sampling efforts were concentrated on peak layer presence between 12 and 27 July. Equipment failure on 21 and 27 July forced me to restrict the microscopic analysis to samples taken on 12, 14, and 19 July. Additional surveys examined the presence of layers on 6 June, 30 August, and 3 October 2005.

Sampling. The weather on all sampling days was calm and sunny. At each station, the water column was profiled with a SeaBird 19+ CTD with mounted fluorometer to collect continuous profiles of temperature,

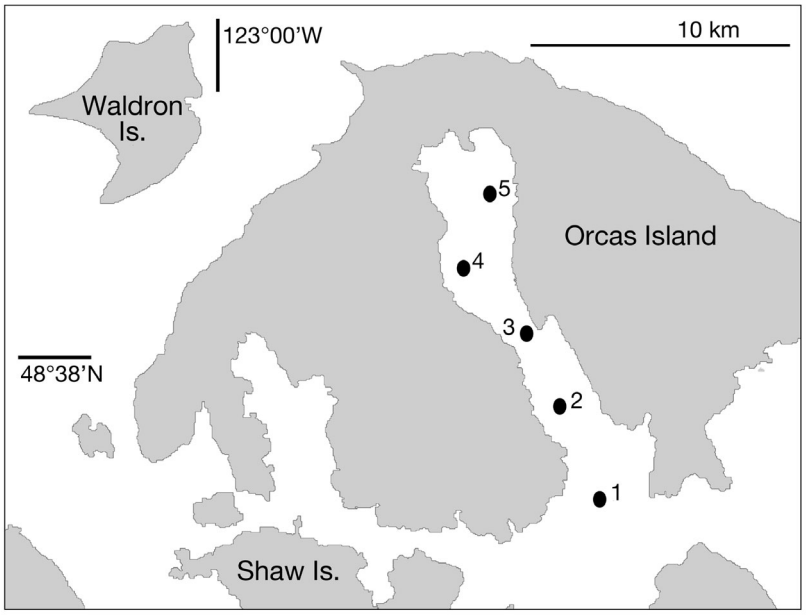

Fig. 1. East Sound, Orcas Island, Washington, USA, with the approximate locations of stations sampled between June and October 2005. Stn 1 served as a reference station located just outside a sill restricting water exchange between East Sound and surrounding waters

salinity, and chl *a* fluorescence. The fluorometer model was either a Turner SCUFA or a WetLabs WetStar. The mean descent rate of the CTD was 0.2 m s^{-1}, and the vertical resolution was 0.1 m. Real time measurements of the profiles, including chl *a* fluorescence, were displayed onboard and were used to identify the presence and depth of distinct layers. For the purpose of shipboard identification and choice of target depths, a sharp gradient in fluorescence that exceeded the overall fluorescence of the remainder of the water column was termed a layer. The observed structures did not appear to be artefactual spikes, nor were they destroyed during casting, as evidenced by excellent agreement between the down- and up-casts. Only steep, vertical gradients in fluorescence were used as the identifying layer characteristic. The vertical extent, or thickness of the layer, was not used as a criterion. Some of the layers exceeded 2 m in thickness and thus did not fit the characterization of 'thin layers' by Dekshenieks et al. (2001) for the same locality. Here, the term 'plankton-rich layers' (PRLs) is used to describe layers of high plankton biomass with variable vertical extent that were bordered by steep gradients in plankton concentrations.

Based on the real-time water column profiles, whole water samples were collected from 2 depths, one within the fluorescence maximum (between 5 and 9 m) and one below (between 10 and 20 m) using a horizontally mounted, 2 l Niskin bottle. The samples were stored at surface water temperatures in a dark cooler. Triplicate subsamples were withdrawn for shipboard measurements of *in situ* fluorescence with a Turner fluorometer to verify layer capture. In the laboratory, the concentration of extracted chl *a* was determined from triplicate samples (Lorenzen 1966, Strickland & Parsons 1972). Also, 250 ml of whole seawater were preserved with acid Lugol's iodine (Throndsen 1978) at a final concentration of 2%. A total of 100 to 200 cells, >5 µm in size, of the most abundant species were counted in a Sedgwick-Rafter slide (1 ml volume). Abundance of rare species (<100 ml^{-1}), primarily heterotrophic protists, was determined by settling 10 to 50 ml of sample volume following Utermöhl (1931). Species identification was based on Horner (2002). The methods of sampling and microscopic analysis used here were not suitable to quantify the abundance of marine snow, although marine snow was an important constituent of previously observed layers at the same locality (Alldredge et al. 2002). Two-dimensional cell size measurements of 30 to 100 cells were obtained with Image-Pro Plus software to calculate cellular carbon content for each species (Menden-Deuer & Lessard 2000).

Data analysis. Regression analyses were based on a linear, type I model. Similarities of plankton community composition and association were explored using multivariate analyses in PRIMER (Plymouth Routines In Multivariate Ecological Research) v5 using the Bray-Curtis similarity coefficient on square-root transformed biomass data. The conclusions were not sensitive to the type of coefficient or transformation. To determine statistical significance among samples, 10^4 random permutations of the sample data were compared to the observations using ANOVA. All analyses were assigned statistical significance at $p < 0.05$.

RESULTS

Water column profiles and PRLs

Distinct layer structures in fluorescence profiles were observed during surveys between 12 and 27 July 2005. A progression of CTD profiles from a 5-station transect up East Sound on 14 July 2005 shows the increasing thermal stratification and concurrent increase in structuring of the fluorescence signal (Fig. 2). Profiles on 6 June and 30 August revealed distinct thermal stratification of the water column, but no corresponding PRLs,

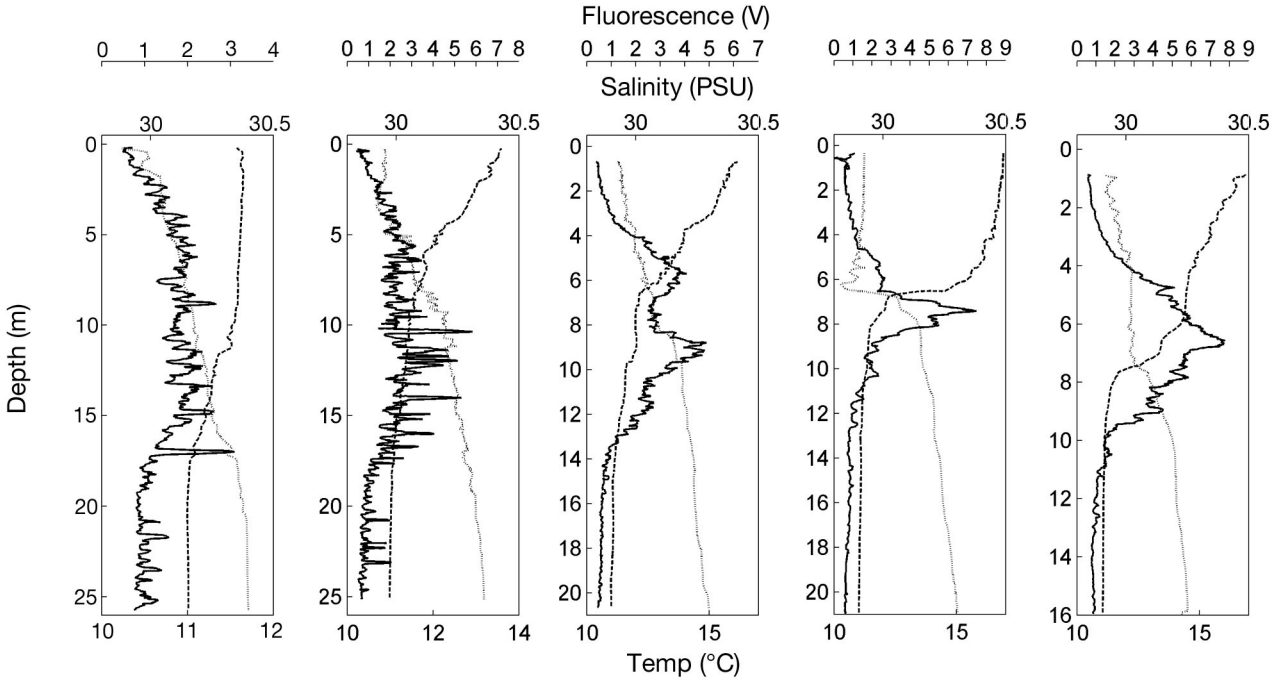

Fig. 2. Vertical CTD profiles of temperature (dashed line), salinity (dotted gray line), and chlorophyll *a* (chl *a*)-induced fluorescence (solid line) from a 5 station transect on 14 July 2005. Profiles are arranged in order from Stns 1 to 5, south to north, with the first profile representing Stn 1 just outside East Sound. Note difference in scales. Plankton-rich layers (PRLs) were observed in 80% of the casts within the temperature-stratified sound during the summer months. No layers were ever observed at Stn 1, outside East Sound

despite abundant (visible to the naked eye) colonies of *Chaetoceros socialis*. On 3 October, no thermal stratification was observed, and plankton abundance in the water column was very low. No distinct layers were ever observed at the station outside of East Sound. It is noteworthy that both within and outside East Sound, the distribution of chl *a*-induced fluorescence was highly variable, even if a distinct layered structure was not observed (Fig. 2, Stn 1).

In July, the water column was thermally stratified. A decrease in surface salinity was seen on 19 July, presumably due to the influx of river water originating from the Fraser River in the Strait of Georgia (Hickey et al. 1991). All layered structures were observed in close association (within 1 to 2 m) with the pycnocline, located above, below or coinciding with it. Layers ranged in thickness from <1 m to several meters and even included structures with distinct double peaks (Fig. 2, Stn 3). Fluorescence within layers exceeded background by up to 7-fold. Extracted chl *a* ranged from 1.3 to 23.1 µg l^{-1} chl *a*.

Phytoplankton biomass correlated with fluorescence

All proxy measurements of phytoplankton abundance, from CTD mounted fluorometer-derived fluorescence, to immediate, shipboard measurements of sample fluorescence, extracted chl *a*, and microscopy-based plankton biomass were significantly correlated (Fig. 3, Table 1). This indicates that a CTD-mounted fluorometer was an

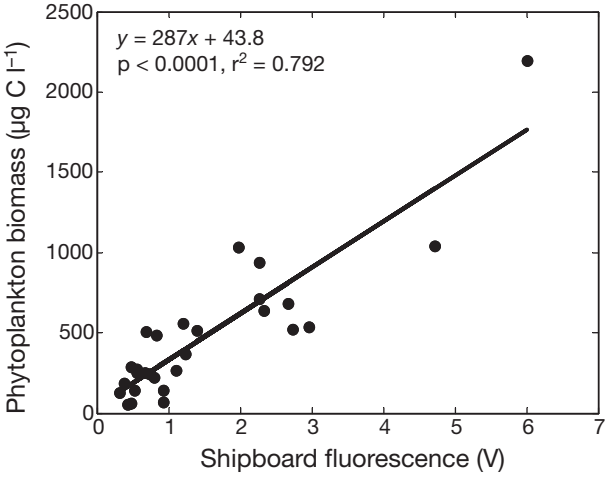

Fig. 3. Correlation between chlorophyll *a* (chl *a*)-induced fluorescence, measured immediately after sample collection, and microscopically determined plankton C biomass. A significant, positive correlation was observed for all measures of plankton abundance from *in situ* fluorescence, extracted chl *a*, to microscopy-based biomass estimates

appropriate tool for identifying the meter-scale PRLs and that the chosen sampling methods were appropriate to capture water from those layers.

Plankton community composition

Microscopic identification of the plankton communities within and outside the layers showed that members of the diatom genus *Chaetoceros* were by far the most abundant species, both in terms of cell numbers and biomass (Table 2). The most frequently encountered species were, in order of decreasing biomass, *C. debilis*, *C. decipiens,* and *C. socialis*. *Chaetoceros* species dominated the community both within and outside PRLs, contributing on average 50% of the total phyto- and zooplankton biomass (range 3 to 96%). *Pseudo-nitzschia* spp., *Eucampia zodiacus*, and *Skeletonema costatum* were at times abundant, contributing up to 20% of the total plankton biomass. *Pseudo-nitzschia pseudo-delicatissima* concentrations averaged 60 cells ml^{-1}, with maximum abundances of 260 cells ml^{-1}. Other, frequently encountered species that comprised less than 5% of total biomass were the diatoms *Thalassiosira* spp. and *Ditylum brightwellii* as well as the mixotrophic dinoflagellate *Ceratium furca*. Heterotrophic protists contributed less than 5% of the total biomass (range 1 to 10%). The most abundant heterotrophic protists included several *Protoperidinium* and *Gyrodinium* spp., and several oligotrich ciliates, e.g. *Strombidinopsis* sp., *Mesodinium* sp., and *Laboea* sp. Silicoflagellates were not counted but were at times abundant.

Table 1. Coefficients from regression analyses among independent measures of phytoplankton abundance: shipboard measurement of CTD fluorescence (ShipF), extracted chlorophyll *a* (chl *a*), and microscopy-based biomass estimates of plankton samples (PBiomass)

Source data	Slope	*y*-intercept	p	r^2	n
ShipF:chl *a*	0.266	−0.126	<0.0001	0.88	32
ShipF:PBiomass	287	44	<0.0001	0.79	26
Chl *a*:PBiomass	85	−38	<0.0001	0.86	26

Table 2. Biomass (µg C l^{-1}) of dominant plankton species in the size range >5 and <200 µm in samples taken at depths within and outside plankton-rich layers (PRLs) between 12 and 19 July 2005. Carbon biomass was calculated from linear cell size measurements using taxon-specific equations (Menden-Deuer & Lessard 2000)

Stn	Depth (m)	Thecate dinofl.	Athecate dinofl.	Ciliates	*Chaetoceros debilis*	*C. socialis*	*C. decipiens*	*Pseudo-nitzschia* spp.	*Eucampia zodiacus*	*Skeletonema costatum*
12 July										
1	5	5.7	2.2	1.0	29	15	0.0	11	410	5.9
1	15	25	7.7	5.0	105	28	27	38	201	53
2	5	8.8	12	4.7	68	61	17	53	752	47
2	15	3.1	2.8	2.0	0.9	3.7	0.0	7.1	114	8
3	6	5.8	9.9	6.1	109	138	58	85	0.0	185
3	15	2.1	2.2	1.5	5.2	6.4	0.0	9.1	142	12
4	6	13	14	14	67	95	15	110	0.0	202
4	15	0.9	0.8	1.0	0.0	9.9	0.0	4.2	0.0	26
14 July										
1	5	2.8	1.6	1.4	71	101	14	8.9	65	15
1	15	6.9	1.6	1.3	70	97	13	12	40	11
2	9	13	3.1	4.6	136	0.0	7.2	45	17	13
2	20	1.6	4.3	2.3	14	58	18	20	52	16
3	7	5.9	5.7	3.7	276	113	11	68	0.0	14
3	15	1.5	1.9	2.2	11	3.8	1.4	16	26	23
4	8	8.4	5.5	6.1	85	215	48	70	0.0	41
4	15	3.4	0.5	1.7	1.4	1.7	0.0	13	0.0	43
5	5	7.2	11	5.2	107	112	20	25	0.0	18
5	15	2.8	1.6	1.4	5.4	21	6.0	13	0.0	23
19 July										
1	5	1.5	0.3	0.8	54	0.0	71	11	0.0	20
1	15	1.0	0.2	0.5	62	129	10	8.5	0.0	28
2	6	10	0.7	2.3	330	191	158	8.5	0.0	0.0
2	15	2.9	0.2	1.0	46	104	26	5.7	0.0	15
3	5	12	1.8	1.8	1584	384	0.0	30	0.0	170
3	15	4.0	2.1	0.9	335	101	38	23	0.0	5.0
4	6.5	25	12	1.2	219	280	432	117	0.0	0.0
4	15	11	8.7	2.8	297	127	17	163	0.0	88

The abundance, biomass, and species composition of both phytoplankton and heterotrophic protists were compared to investigate the spatial and temporal coherence of the plankton communities, particularly within PRLs. The results from analyzing spatial patterns in community composition showed that no significant differences were observed between the species composition of samples taken within PRLs (5 to 9 m depth) and samples taken outside PRLs (10 to 20 m depth). Comparing species distributions at different stations showed considerable variability (±100%) in biomass throughout the fjord. The maximum recorded plankton biomass, over 2000 µg C l^{-1}, was found at the central station Stn 3. Despite these differences in biomass, no significant differences in the composition and biomass of the species were observed among all stations on any one sampling day (Fig. 4A, p = 0.55). If the km-scale spatial resolution was sufficient, these results indicate that for each cruise day, layers were coherent and continuous over the sampled area within East Sound. Comparing species composition over the course of the sampling week (12–19 July) showed significant changes in community composition with time (Fig. 4A, p = 0.02, Table 2). No significant difference (p = 0.06) in species composition was observed between 12 and 14 July. This indicates that the layer was continuous in both space and time over those 2 d, although species abundance did change between those 2 dates. *Eucampia zodiacus* biomass was reduced 10-fold, whereas *Chaetoceros debilis* and *C. socialis* biomass nearly doubled over 2 d. Significant (p = 0.018) changes in species composition and biomass were observed between 14 and 19 July, when *E. zodiacus* biomass was reduced to below detection limit, and the biomasses of *C. debilis* and *C. socialis* doubled and quadrupled, respectively (Table 2).

Biomass of heterotrophic protists was dominated by dinoflagellates, contributing on average 80% of the heterotrophic biomass measured. Ciliates contributed on average 20% of the heterotrophic biomass, with a maximum of 40% in a single sample. The heterotrophic dinoflagellate genus *Protoperidinium* contributed on average 50% of the heterotrophic biomass, with a maximum of 77%. Athecate dinoflagellate biomass was dominated by *Gyrodinium* and *Gymnodinium* species.

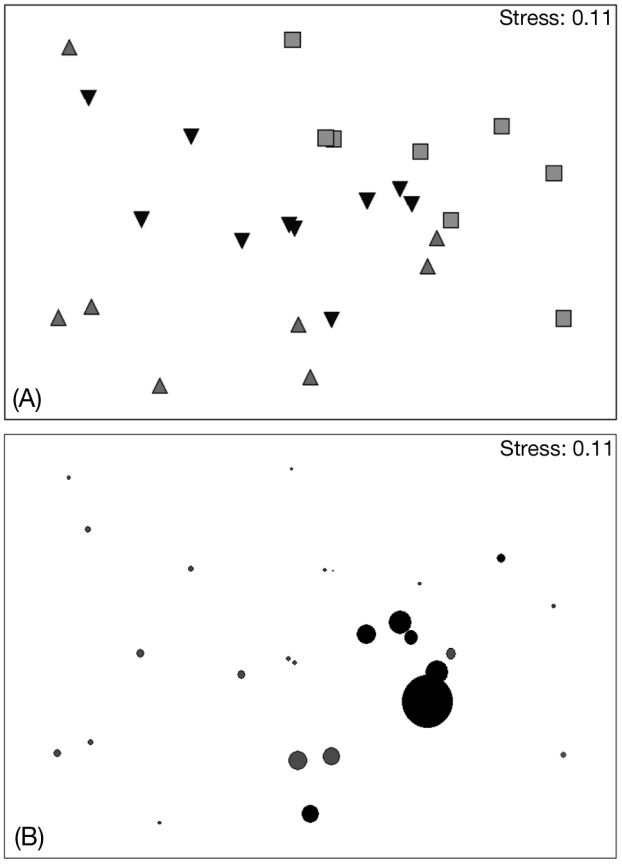

Fig. 4. (A) Non-metric, multidimensional scaling analysis of plankton community composition on 12 (▲), 14 (▼), and 19 July (■) 2005. The distance between samples is proportional to their similarity (rank order difference). Samples from the same date grouping together indicate their relatively greater similarity to each other than to samples collected on other dates. (B) Reproduction of (A) indicating layer intensity (i.e. the ratio of plankton biomass within and outside the fluorescence maximum) and heterotrophic biomass for each sample. Samples with layer intensity >3 shown in black; samples without a distinct structure in fluorescence profile (layer intensity <3) shown in grey. Circle diameters are proportional to heterotrophic protist biomass with the largest diameter corresponding to the largest protist biomass. Larger heterotrophic biomass was observed within layers, but no significant correlation between layer intensity and biomass was found for the dominant phototrophic species (see Table 3)

Heterotrophic protists aggregated within PRLs

To quantify the degree of phytoplankton structuring, the ratio between phytoplankton biomass within PRLs relative to the background was calculated, which is termed layer intensity. Samples with layer intensities equal to or exceeding 3 were designated as PRLs. The maximum observed layer intensity was 12.3; thus, over an order of magnitude greater biomass was concentrated within PRLs than in the water below where the background samples were collected. The correlation between layer intensity and protistan predator biomass (dinoflagellates and ciliates) was examined to investigate whether the distribution of predators was related to the observed structuring of phytoplankton distributions. Protist predator biomass showed a strong, positive correlation to layer intensity (Fig. 4B,

Table 3. Correlation coefficients of biomass of several planktonic groups or species and the corresponding layer intensity, i.e. the ratio of plankton biomass within versus outside plankton-rich layers (PRLs)

Taxonomic group	Correlation coefficient	p
All heterotrophic protists	0.793	0.001
Thecate dinoflagellates	0.660	0.001
Ciliates	0.875	0.001
All phytoplankton	0.402	0.025
Chaetoceros debilis	0.182	0.362
Eucampia zodiacus	0.167	0.386

Table 3, p = 0.001) indicating accumulation of predators in the densest parts of the layer. Phytoplankton biomass distributions showed a weaker correlation, with dominant species distributed throughout the water column. These differences in biomass distributions suggest that different processes underlie the structuring of phototrophic and heterotrophic plankton.

DISCUSSION

The temporal and spatial patterns in plankton community composition identified in this study suggest that on each sampling day, a continuous plankton layer extended throughout, but not beyond, the fjord. The layers contained up to 12 times more phytoplankton biomass than surrounding waters. Species composition within PRLs were indistinguishable throughout East Sound on any given sampling day and appeared to be enriched from local sources within East Sound. Higher spatial sampling resolution may well have suggested vertical stratification or patchiness of species (e.g. Montagnes et al. 1999). Comparison of species composition within PRLs to deeper waters did not suggest that layers were advected from outside East Sound.

Dekshenieks et al. (2001) identified that layer presence in East Sound coincided with calm conditions and water column stratification. These physical conditions also apply to the observations reported here. Based on dye experiments off the Oregon Coast and resulting similarities between dye-layers and plankton-layers, Cowles (2004) suggested that vertical shear and shear dispersion may be the most important contributors to layer formation. Recent work on the Oregon shelf further supports this hypothesis (Sutor 2004). The continuous, coherent layers reported here provide further support for the hypothesis that horizontal, physical processes are more important than vertical mixing in the formation of layers.

The temporal dynamics in both species composition and their biomass suggest that layer communities underwent rapid changes on the order of a few days. Interestingly, no physical processes (e.g. advection, mixing) need to be invoked to explain these changes in community composition. Shifts in species abundance and distribution patterns could be entirely explainable through biologically mediated processes; that is, observed increases in biomass could have resulted from growth, and reduction in cell numbers could have been be due to predation or mortality. Even the most dramatic changes in cell concentrations, such as the 10-fold decrease in *Eucampia zodiacus* biomass, are well within the range of ingestion rates measured for the predator species present within the layers (Menden-Deuer et al. 2005). Although it is not documented that *Protoperidinium* species feed on this particular diatom species, the predator will readily feed on other large diatoms. Similarly, increases in cell numbers, such as observed for *Chaetoceros debilis*, could have been the result of growth at 0.46 cells d^{-1}, which is well within the range of observable growth rates (0.10 to 0.76 d^{-1}) for this genus (Leonardos & Geider 2004). Whether these fluctuations in cell numbers are truly attributable to plankton growth and grazing can only be documented through direct measurements of the production and consumption rates of layer-associated plankton communities.

Alldredge et al. (2002) reported a phytoplankton layer largely dominated by *Thalassiosira* spp. in late May 1996. *Thalassiosira* spp. did occur in most samples of the present study, but constituted <1% of the biomass. Instead, samples were dominated by a few *Chaetoceros* species, which contributed up to 95% of the total plankton biomass. These differences in species composition are almost certainly attributable to the difference in timing of the respective cruises. An annual succession pattern of *Thalassiosira* spp. dominating the early community composition, followed by the genus *Chaetoceros* is typically observed in long-term records collected within Puget Sound (Horner et al. 2005, R. Horner pers. comm.). In any case, these observations point out that layer formation is not restricted to a particular phytoplankton species but can be formed by multiple species that may be following a successional pattern.

The layer composition reported here was dominated by medium to large, chain-forming diatom species. Elsewhere, several studies have reported intense, reoccurring layers of phytoplankton of diel-vertically migrating dinoflagellates (Eppley et al. 1968, Kiefer & Lasker 1975). In those studies, the mechanisms of formation and persistence of the layers was due to the behavior of the layer-forming organisms. It is intriguing to speculate that the diatoms dominating the layers observed here could have similar vertical migration behaviors. Based on work by Villareal et al. (1999), ver-

tical movements of diatoms through buoyancy control is certainly a possible formation mechanism.

Comparison of the biomass and distribution of potential phytoplankton prey species to known functional responses of heterotrophic protists suggests that PRLs could serve an important role in the trophic structure of planktonic food webs. Heterotrophic dinoflagellates of the genus *Protoperidinium* were the dominant predators in the analyzed plankton samples. In laboratory experiments, *Protoperidinium* reached maximum growth rates at relatively low prey concentrations (50 µg C l^{-1}), and were able to survive prolonged starvation in the absence of prey (Menden-Deuer et al. 2005). Coincidentally, the concentration of the most abundant prey species, *Chaetoceros debilis*, exceeded the growth threshold of *Protoperidinium* within each of the layer samples, whereas *C. debilis* biomass in waters adjacent to the layers was below the growth threshold of *Protoperidinium* in all but 3 samples. Thus, the population dynamics of this predator could well have been driven by its location relative to PRLs, since phytoplankton concentrations were above the dominant predator's apparent growth threshold only within PRLs (Menden-Deuer et al. 2005).

The concentration of prey in distinct layers and the almost exclusive occurrence of predators within those layers have important ramifications for the trophic dynamics of the system. Predators were not indiscriminately enhanced in areas of higher resource concentration. The more phytoplankton distributions were structured as distinct patches, bounded by steep vertical gradients, the higher the probability of observing predators within rather than outside PRLs. Heterotrophic protists were enhanced in the most intense (i.e. steepest vertical gradient) sectors of the layer. This correlation exists between the degree of structuring in the water column, not the biomass of phytoplankton itself. The importance of the physical or community structure rather than absolute biomass is evident, for example, in the fact that some dominant phytoplankton showed no correlation in their distribution relative to the layer. The probability of observing those diatom species was not affected by the presence of layers. For heterotrophic protists, however, there was a significantly higher probability of detecting heterotrophic species within PRLs. This correlation in predator–prey biomass could either result from growth in place or from aggregation of predators to areas of higher prey concentrations.

Heterotrophic protists can have very high growth rates, leading to rapid increases in biomass (Hansen et al. 1997). I only observed slight increases in either ciliate or dinoflagellate cell numbers over time, but cannot exclude the possibility of predator growth and subsequent consumption through higher-order predators. Large zooplankton were not included in this analysis, although it is undoubtedly important to consider the enhanced biomass of both phytoplankton and heterotrophic protists as rich targets for copepods. Alternatively, predator foraging behaviors could have resulted in an aggregation of predators within PRLs. Menden-Deuer & Grünbaum (2006) have quantified protistan predator movement behaviors in spatially structured prey distributions and predicted the temporal and spatial scales over which prey distribution and predator behaviors could affect trophic and demographic dynamics. The spatial and temporal scales of layer occurrence and persistence observed in East Sound are well within the predicted range of patches accessible to predators exhibiting prey-locating behaviors. Coincidentally, the calm, stratified conditions conducive to layer presence also stabilize the water column for hours to days, which increases accessibility of prey patches to heterotrophic protists by both increasing the timescales of patch persistence (Grünbaum 2001) and providing conditions that facilitate persistent, directional swimming (Karp-Boss et al. 2000). Therefore, aggregation of consumers to PRLs rather than solely growth in place appears a viable alternative to explaining the high degree of correlation between predator and prey biomass.

The correlated predator–prey abundances reported here do not agree with observations by Bjørnsen & Nielsen (1991) of a negative correlation between heterotrophic protists and an intense layer of the phototrophic dinoflagellate *Gyrodinium aureolum*. Note that avoidance of the *G. aureolum* layer by protistan predators may have been due to the 3-fold higher chl *a* concentration or the sometimes ichthyotoxic property of the dinoflagellate, which appears to be a poor quality prey for at least some microplankton predators (Hansen 1995). In contrast, diatoms provide an excellent prey source for many heterotrophic dinoflagellates, including *Protoperidinium* species (e.g. Jeong et al. 2004). Review of the available evidence suggests that specifically heterotrophic dinoflagellates are the dominant grazers of large and bloom-forming diatoms (Sherr & Sherr 2008), which could explain why heterotrophic dinoflagellates dominated the diatom layers. Thus, knowledge of the layer-associated species composition is critical to assess the potential implications of these patches for the dynamics of marine microbial food webs.

Plankton patches, including PRLs, may fundamentally alter trophic and demographic rates of the microbial communities in which they occur and may represent biological hot spots, where trophic and demographic rates are enhanced, resulting in different biological dynamics than can be concluded from average biomass and bulk rate measurements. The data

presented here suggest that biological processes could result in significant changes in layer intensity through phytoplankton growth or grazer-induced mortality. To assess the importance of these processes, the feedback between scales of patchiness and effects on productivity needs to be investigated through empirical measurements of the community production and consumption rates, as well as physical mechanisms like mixing and sinking. For trophic dynamics, the absolute magnitude of phytoplankton biomass within PRLs may be less important than the prey concentration relative to a predator's survival threshold. Ultimately, the mechanisms causing high degrees of spatial variability in phytoplankton biomass need to be understood to predict their effect on the rates of transfer and energy in pelagic microbial food webs.

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