

Seasonal and Spatial Patterns of “Green Tides” (Ulvoid Algal Blooms) and Related Water Quality Parameters in the Coastal Waters of Washington State, USA¹

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Eutrophication-induced macroalgal blooms can impact marine communities, yet little is known about this phenomenon in the northeastern Pacific region. Changes in ulvoid biomass and water quality parameters (nutrients, transparency, temperature, salinity, and oxygen concentrations) were monitored at 6 sites on Blakely Island, Washington State, USA for two years. Observed ulvoid biomass varied from 0 to 441 g dw m⁻². Biomass peaked in summer and autumn and was greatest at sites with the highest water-column nitrogen concentrations. Intertidal ulvoid communities were dominated by *Ulva fenestrata* Postels et Ruprecht while *Ulvaria obscura* (Kützinger) Gayral dominated the subtidal zone near Blakely Island. In contrast with these observations, prior quantitative studies describe *Ulvaria* as rare or ephemeral. Fifteen additional sites were examined for species composition patterns. Similar patterns were seen at sites in Puget Sound, while *Enteromorpha* spp. were more common and *U. obscura* absent at sites in Hood Canal, Willapa Bay, and Grays Harbor. Green tides and other macroalgal blooms are typically reported to be monospecific, while in the present study two or more species are in close association, albeit at different tidal elevations. *Enteromorpha* spp. and *Ulva* spp. are known as important components of green tides, but relatively little is known about the biology of *Ulvaria*. Substantial variation in biomass on a fine geographic scale indicates the need for fine scale monitoring of the green tide phenomenon in the northeastern Pacific region.

Introduction

This study examines the species composition and seasonality of “green tides” (i.e., blooms of ulvoid macroalgae including *Enteromorpha* Link, *Monostroma* Thuret, *Ulva* (L.) Thuret, and *Ulvaria* Ruprecht spp.) in the northeastern Pacific region. Macroalgal blooms have been blamed for eradicating seagrass meadows, altering faunal community structure, and creating unsightly, malodorous piles on beaches (e.g., Valiela *et al.* 1997, Hauxwell *et al.* 2001). They are extremely productive, albeit ephemeral, communities. Blooms are often associated with eutrophication (e.g., in the Venice lagoon), although a variety of abiotic and biotic factors may limit ulvoid algal abundance and productivity (Kida 1990, Henley *et al.* 1991, Geertz-Hansen *et al.* 1993, Rivers and Peckol 1995, Anderson *et al.* 1996). Problematic macroalgal blooms are typically reported to be monospecific (Valiela *et al.* 1997), although species composition may be dependent on environmental conditions (Lotze and Schramm 2000).

The genera involved in “green tides” are superficially similar, despite significant differences in life cy-

cles and developmental patterns, and can be impossible to distinguish reliably in the field. The three Ulvacean genera (*Enteromorpha*, *Ulva*, and *Ulvaria*) have isomorphic gametophytic and sporophytic stages. In contrast, the bladed form of *Monostroma* is the larger gametophytic stage in a heteromorphic life cycle (Bold and Wynne 1985). At least part of the *Enteromorpha* thallus is tubular. *Ulva* is an entirely flat, distromatic blade. *Ulvaria* and *Monostroma* are both monostromatic blades (Gabrielson *et al.* 2000). The variety of *Ulvaria* found in the northeastern Pacific region [*U. obscura* v. *blyttii* (Areschoug) Bliding] darkens to olive drab or black on drying allowing it to be distinguished from *Monostroma* (Scagel *et al.* 1989).

Little is known about the causes, extent, or history of ulvoid blooms in this region (Bulthuis 1991). Anecdotal evidence suggests that significant interannual variation in the intensity of the blooms occurs in some locations, while ulvoid algae are always abundant during the summer at other sites (T. Mumford, personal communication). Areas with excessive green algal growth elicit odor-related complaints from waterfront residents (G. Frankenstein, personal communication) and blooms can be sufficient to inhibit the growth of eelgrass (*Zostera marina* L., Nelson and Lee 2001). Problematic blooms of green algae are not, however, associated with locations

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thought to be at high risk of eutrophication (Dowty 2002).

The region considered includes the Straits of Juan de Fuca, Puget Sound, and 2 large coastal bays in Washington State, USA (Fig. 1). The maximum tidal range is approximately 4–5 m through much of this

area, though the amplitude is reduced in the southern (i.e., landward) reaches of Puget Sound (Kawaky 1999). Water transparency is often low, and light limits the extent of subtidal plant communities. The combination of cloudy weather, shorter daylengths (as low as 8L:16D), and increased mean tidal height

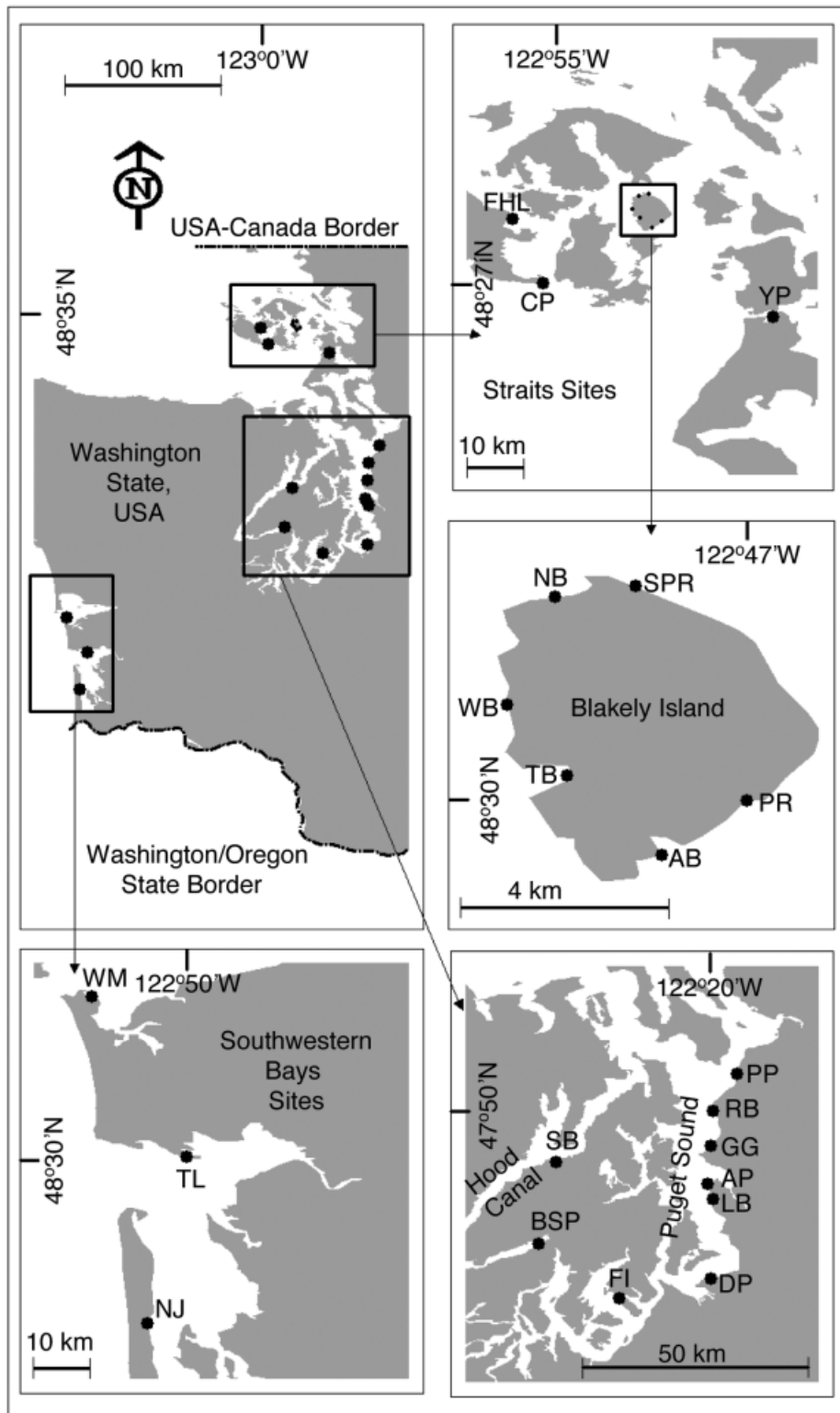


Fig. 1. Map of sampling sites near Blakely Island, Washington State, USA.

during daylight hours can result in a 100-fold decrease in light available to subtidal communities from summer to winter (Nelson and Waaland 1997). Nutrient concentrations are usually high and algal growth luxuriant, although both decline during El Niño years (Nelson 1997, Dowty 2002). Common macroalgal grazers include snails, several species of urchins, and chitons (e.g., Vadas 1977, Nelson and Waaland 1997).

Anthropogenic impacts affect the entire region. Approximately 4.0×10^6 people were living in the counties bordering Puget Sound in 2000, an increase of 21% since 1990 (United States' Bureau of the Census 2002). The largest human population centers are in central Puget Sound (e.g., sites LB, AP, and GG in Fig. 1), and populations of lingcod [*Ophiodon elongatus* (Girard), Osteichthyes: Chordata] and pigeon guillemots [*Cephus columba* (Pallas), Aves: Chordata] are substantially lower in this area than to the north or south (Dowty 2002). Diversity of intertidal marine invertebrates, however, appears to decrease from north to south (i.e., seaward to landward) in Puget Sound. Among the sites examined, the southwestern bays (Fig. 1) are the most removed from large population centers yet are the location of the most intense aquaculture in the area (primarily oyster farming) and have been subjected to substantial forestry and agricultural activities, including extensive diking (Dowty 2002). Commercial and sport-fishing are common throughout the area, groundfish populations are depressed, and several salmonid stocks have been listed as threatened under the United States' Endangered Species Act. Fish species with little value to commercial or sport fishers remain abundant (Musick *et al.* 2000).

This study was conducted in two phases. In the first phase, physical, chemical and biological parameters typically associated with green tides (Kida 1990, Henley *et al.* 1991, Rivers and Peckol 1995, Valiela *et al.* 1997) were measured quarterly for 2 years at 6 sites in a restricted geographic area (offshore of Blakely Island, Washington State, USA). In the second phase, biomass and species composition were measured during the summer of 2000 at 15 sites over a larger geographic area. The aim of the study was to elucidate how biomass and species composition of ulvoid algal blooms varied with depth, sampling date, and location. Furthermore, this study aimed to identify which physical or chemical parameters best predict temporal and spatial changes in biotic variables.

Material and Methods

Phase I: intensive sampling near Blakely Island

Biological, physical, and chemical parameters were measured quarterly at 6 sites in the vicinity of Blakely Island, Washington, USA (Fig. 1). Seal Pup Rock (SPR, 48°35.2'N, 122°47.9'W), Pinnacle Rock (PR,

48°32.6'N, 122°47.1'W) and Armitage Bay (AB, 48°32.2'N, 122°48.0'W) are on the Rosario Strait side (east) of Blakely Island and thus are exposed to high currents as water moves from the Strait of Juan de Fuca to the Straits of Georgia. The SPR site is protected from wave action by two small islands, while PR is more exposed. AB is in embayment with a sheltering island (Armitage Island) at the mouth of the bay. PR has a steeper slope than any of the other sites (30% versus ≤5% at all 5 other sites). West Beach (WB, 48°33.7'N, 122°49.8'W) and Thatcher Bay (TB, 48°33.1'N, 122°49.0'W) are on the Lopez Sound side (west) of Blakely Island and are thus much more protected. Current speed is low and water exchange minimal on this side of the island. TB is the former site of a sawmill (closed in 1951) and there are substantial quantities of sawdust in the intertidal zone. Wave action is lower at TB than at WB. North Bay (NB, 48°35.0'N, 122°49.1'W) is on a channel connecting Rosario Strait and Lopez Sound. Water flow through this channel can be rapid during spring tides but the site is protected from significant wave action.

Sampling began in June 1998 and continued through March 2000. "Spring" samples were collected in mid-March, "summer" samples in late June 1999 or early July 1998, "autumn" samples in mid-September, and "winter" samples in mid-December 1998 or early January 2000. All 6 sites were sampled within a 1 week period. The sampling order was determined randomly, except when wind events prevented safe diving at some sites and the random sequence was altered.

Species-specific biomass was determined at 0 m, -1 m, and -2 m MLLW (mean lower low water) on each sampling date. To determine biomass at each depth, all ulvoid algae were removed from five square 0.1 m² quadrats and returned to the laboratory. Quadrat locations were selected randomly along a 50 m isobath and noted on the divers' slates prior to collection. *Enteromorpha* spp. were identified, dried and weighed. Since *Ulva*, *Ulvaria*, and *Monostroma* spp. resemble each other and might be found at these sites we estimated the contribution of these species by positive identification of each algal thallus prior to drying and weighing. All specimens were cross-sectioned and a small piece was preserved on herbarium paper. These voucher specimens were subsequently deposited in the Seattle Pacific University Herbarium. If more than 10 thalli were present in any one quadrat (as was common), only 10 haphazardly selected fragments were positively identified. The proportion of the biomass attributable to each species was estimated by dividing the number of blade fragments of that species by the total number of blade fragments identified. This proportion was multiplied by the total biomass of ulvoid algae at the site to find the species-specific biomass.

Several physical and chemical water quality variables were measured at each site and sampling date.

The coefficient of light extinction in the water column was determined from light intensity measured at the surface and at 0.5 m intervals to the substratum or a maximum depth of 5 m (LI 1000 meter and spherical quantum sensor, LI-COR, Lincoln, NE, USA). Temperature and oxygen concentration were similarly measured at 0.5 m intervals using an oxygen electrode and meter (YSI 57 meter and 5739 probe). Temperature data are reported as surface temperature (the average of measurements at 0, 0.5, and 1 m below the surface) and stable temperature (the temperature which does not change with increasing depth up to 5 m deep). Salinity was measured at the surface using a salinity refractometer (model RHS-10, Westover Scientific, Woodinville, WA, USA). Preliminary measurements indicated that salinity did not change from the surface to the maximum depth at any of our sites. Three surface water samples were collected, filtered, and frozen for nutrient analyses. Nutrient analyses (NO_3^- , NO_2^{2-} , NH_4^+ , PO_4^{3-} and $\text{Si}(\text{OH}_4)^-$) were conducted by the Chemical Oceanography Laboratory, University of Washington (using techniques described in Whitley *et al.* 1981). Dissolved inorganic nitrogen (DIN) was assumed to be the sum of NO_3^- , NO_2^{2-} , and NH_4^+ concentrations. Daylength (the time from sunrise to sunset) was noted on each sampling date.

Multidimensional scaling (MDS) was used to group sites with highly correlated physical-chemical environments. Most physical and chemical parameters were tested using a two-way ANOVA with sampling dates and sites treated as fixed factors. Data were initially examined with Levene's test for heteroscedasticity and the Shapiro-Wilk test for normality. Based on these preliminary analyses, we used \ln transformation on [oxygen], temperature, and DIN prior to ANOVA. Water transparency, as measured by the coefficient of extinction, was analyzed using a block design ANOVA with sampling dates as the blocking factor and sites as a fixed factor. Transparency data were square root transformed to eliminate interaction effects as determined by Tukey's 1 degree of freedom for nonadditivity test (Neter *et al.* 1985). The Student-Newman-Keuls post-hoc multiple comparison test was used if ANOVA indicated a significant effect of any factor. Differences between treatment means are described as "significant" if $\alpha < 0.05$.

Biomass and species composition were tested using a 3-way ANOVA with sampling dates, sites, and depth treated as fixed factors. Biomass data and the proportion of biomass attributable to *Ulvaria* both showed substantial inequality of variance. Biomass data were square-root transformed and proportional data were arcsine (square root) transformed to reduce, although not completely eliminate, this heteroscedasticity. The Games-Howell post hoc test was employed in both cases because it does not assume equality of variance. The SPSS 10.0.5 software pack-

age was used to perform statistical analyses (SPSS, Inc., USA, 1999).

Correlations between biotic and abiotic variables were found after averaging biomass measurements over all 5 replicates at each depth. This removed quadrat to quadrat variation from the analysis. Path analysis, a regression technique using standardized variables, was employed to examine the effects of multiple factors on biomass (Li 1975). The path coefficients (denoted p) calculated by this method reveal the relative contribution of each independent variable to the dependent variable. The results are plotted as a path diagram showing path coefficients between independent variables and biomass and regression coefficients between independent variables.

Phase II: biomass and species composition at a larger geographic scale

During the summer of 2000, biomass and species composition were determined at 15 sites between Willapa Bay and the San Juan Island Archipelago (Fig. 1). These sites can be grouped into 3 geographic regions as follows: 1) Southwestern Bays (Westport Marina [WM, 46°54.2'N, 124°05.9'W], Tokeland [TL, 46°42.2'N, 123°58.6'W], and Nahcotta Jetty [NJ, 46°30.1'N, 124°01.6'W]), 2) Puget Sound (Fox Island [FI, 47°16.5'N, 122°39.2'W], Dash Point [DP, 47°19.3'N, 122°24.8'W], Lowman Beach [LB, 47°32.4'N, 122°23.8'W], Alki Point [AP, 47°34.7'N, 122°24.8'W], Golden Gardens [GG, 47°41.7'N, 122°24.2'W], Richmond Beach [RB, 47°46.5'N, 122°23.6'W] and Picnic Point [PP, 47°52.8'N, 122°19.9'W]), Hood Canal (Seabeck [SB, 47°38.6'N, 122°49.4'W] and Belfair State Park [BSP, 47°25.6'N, 122°52.6'W]) and 3) the Straits (Yokeko Point [YP, 48°24.8'N, 122°37.4'W], Friday Harbor Laboratories [FHL, 48°32.7'N, 123°00.6'W], and Cattle Point [CP, 48°27.3'N, 122°57.7'W]). Biomass and species composition were determined at 0, -1, and -2 m MLLW as described for sites examined during Phase I.

Results

Phase I: physical and chemical parameters

Multidimensional scaling indicated a difference in water quality between the Lopez Sound sites on Blakely Island and the Rosario Strait sites (Fig. 2). The Rosario Strait sites (AB, PR, and SPR) formed a group in the fourth quadrant. Site NB, on the channel connecting Lopez Sound and Rosario Strait, was the site closest to this cluster. The Lopez Sound sites (TB and WB) were in the second and third quadrants and farther from the cluster of Rosario Strait sites.

A closer examination of measured water quality parameters illustrates the patterns seen in the MDS. Significant, albeit often small, variations between

sites and dates were found for DIN ($F_{5,96}=154.6$, $p < 0.0005$ and $F_{7,96}=737.6$, $p < 0.0005$, respectively) phosphate ($F_{5,96}=25.8$, $p < 0.0005$ and $F_{7,96}=334.3$, $p < 0.0005$, respectively), surface water temperature ($F_{5,94}=17.1$, $p < 0.0005$ and $F_{7,94}=392.1$ respectively), and oxygen concentration ($F_{5,96}=58.0$, $p < 0.0005$ and $F_{7,96}=397.6$, $p < 0.0005$) (Table I). Post hoc multiple comparison tests indicate that sites on the Lopez Sound side of Blakely Island (TB and WB) had significantly lower DIN and phosphate concentrations and significantly higher water temperature and oxygen concentrations than those on the Rosario Strait side (AB, PR and SPR, see Table I for mean values and ranges). Across all sites, DIN and phosphate were lowest, and oxygen concentrations were high-

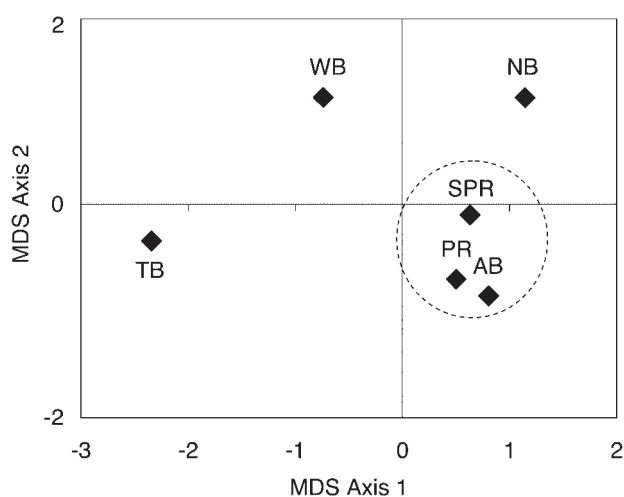


Fig. 2. MDS analysis showing ordination of sites based on physical-chemical parameters. The final iteration had stress = 0.0136 and $R^2=0.99$.

est, during summer and autumn ($1.08\text{--}24.93$ μM DIN, $0.68\text{--}2.08$ μM phosphate, and $9.66\text{--}10.46$ $\text{mg O}_2 \text{ L}^{-1}$) and vice versa in spring and winter ($13.98\text{--}29.14$ μM DIN, $1.67\text{--}2.45$ μM phosphate, and $6.93\text{--}8.78$ $\text{mg O}_2 \text{ L}^{-1}$). Although the average surface water temperature was highest at the Lopez Sound sites (TB and WB), this averaging across all sampling dates obscures an interesting annual pattern: the Lopez Sound sites (TB and WB) were warmer in the summer and cooler in the winter than the Rosario Strait sites (AB, PR, and SPR).

Salinity ranged from 27–32 PSU (averaging 31 PSU) but did not vary significantly from site to site (Table I, $F_{5,96}=1.3$, $p = 0.265$). Variation in water transparency between sites was significant (Table I, $F_{5,29}=2.6$, $p = 0.049$), but specific site-to-site differences could not be distinguished in post hoc tests. The three Rosario Strait sites tended to have clearer water while NB and the Lopez Sound sites had murkier water (Table I). Transparency was greatest in the spring and winter (mean $k_z = 0.33 \text{ m}^{-1}$ and 0.36 m^{-1} , respectively) and lowest in the summer and autumn (mean $k_z = 0.44 \text{ m}^{-1}$ and 0.58 m^{-1} , respectively).

Phase II: Biomass

Ulvoid algal biomass varied with site, sampling date, and depth (Fig. 3). The site \times sampling date \times depth interaction effect was highly significant ($F_{70,576}=8.66$, $p < 0.0005$). The highest biomass (averaged across sampling dates and depths) was recorded at AB, SPR and NB (54.6 , 49.5 , and 29.3 g dw m^{-2} , respectively), followed by WB and PR (12.4 and 16.8 g dw m^{-2} , respectively), and TB (0.6 g dw m^{-2}). Biomass was low-

Table I. Physical/chemical characteristics of phase I sample sites.

	Seal Pup Rock	North Bay	West Beach	Thatcher Bay	Armitage Bay	Pinnacle Rock
Mean DIN (μM)	21.90	20.47	19.39	18.94	22.51	22.81
(range)	(14.24–28.63)	(9.55–28.23)	(1.17–26.73)	(5.04–27.84)	(17.20–28.86)	(17.92–27.01)
Mean N:P	11.47	10.12	9.68	9.64	10.90	11.07
(range)	(9.38–17.38)	(5.41–11.71)	(1.72–11.90)	(5.83–11.84)	(9.50–12.00)	(10.13–11.60)
Mean coefficient of extinction, m^{-1}	0.380	0.505	0.438	0.549	0.377	0.357
(range)	(0.225–0.608)	(0.308–0.878)	(0.294–0.698)	(0.268–1.069)	(0.150–0.764)	(0.244–0.624)
Mean surface temp. ($^{\circ}\text{C}$)	10.1	10.1	10.8	11.2	10.3	10.0
(range)	(8.1–12.0)	(8.0–12.2)	(7.9–15.7)	(7.9–16.8)	(8.1–11.9)	(8.0–11.8)
Mean bottom temp. ($^{\circ}\text{C}$)	9.7	9.8	9.9	10.2	9.9	9.7
(range)	(8.0–12.0)	(7.9–11.7)	(7.9–12.3)	(8.2–12.6)	(8.0–11.7)	(8.0–11.8)
Mean salinity (PSU)	31	31	31	31	31	31
(range)	(29–32)	(30–32)	(30–32)	(28–32)	(29–32)	(29–32)
Mean oxygen (mg/L)	8.37	9.08	9.78	9.12	8.36	8.66
(range)	(6.63–10.10)	(6.80–10.67)	(6.78–15.60)	(6.55–13.00)	(6.02–11.00)	(8.66–11.38)

Values reported are means and ranges across multiple sampling dates.

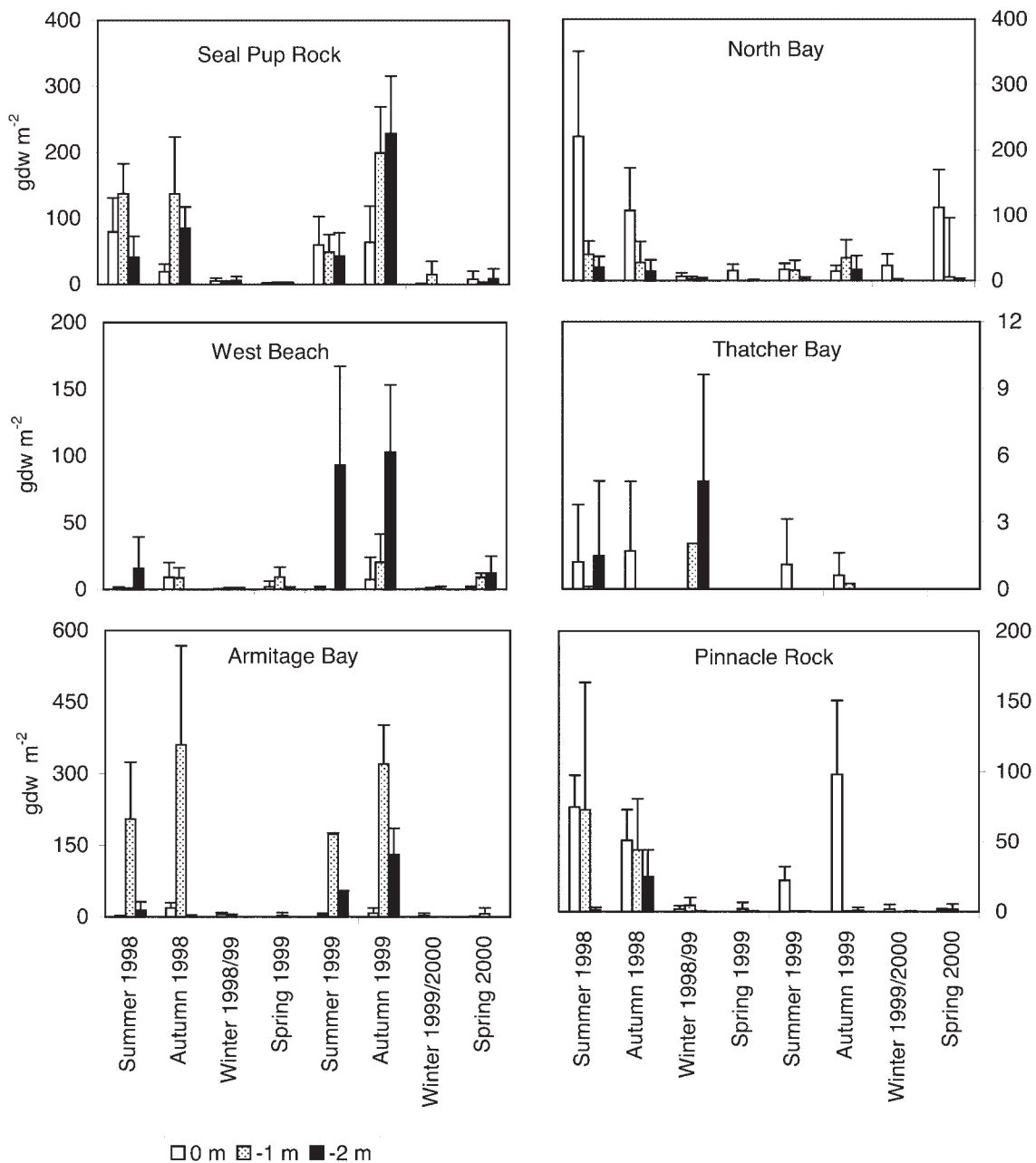


Fig. 3. Temporal, geographical, and elevational differences in ulvoid algal biomass. The y-axis scale is different for each site. Error bars are ± 1.0 SD.

est in the winter and spring (averaging 2.5 and 5.7 g dw m^{-2} , respectively) and highest in the summer and autumn (averaging 35.6 and 59.9 g dw m^{-2} , respectively). Site-to-site differences in biomass were minimal on winter and spring sampling dates and more obvious during summer and fall. The greatest mean biomass was found at -1 m (averaging 39.9 g dw m^{-2}), with substantially less at 0 and -2 m (22.3 and 19.4 g dw m^{-2} , respectively). This general trend masks important differences between sites and sampling dates. Only site AB consistently had the highest biomass at -1 m, while SPR and NB occasionally followed this pattern. Other sites typically had the highest biomass at 0 m (PR), -2 m (WB), or had such low biomass that

any pattern is trivial (TB). During winter and spring, peak biomass was consistently at 0 m, while in summer and fall it was more likely to be at -1 m.

Biomass was significantly positively correlated with daylength and water temperature ($r^2=12.0\%$ and 8.9% , respectively) and significantly negatively correlated with oxygen concentration ($r^2=10.0\%$, Table II). DIN was negatively, but not significantly correlated with biomass ($p=0.07$, $r^2=2.6\%$). Path analysis indicates that the combination of daylength, temperature, and DIN yields the best prediction of biomass ($r^2=17.9\%$ with $p=0.513$, 0.168 , and 0.414 , respectively) (Fig. 4). Low r^2 values throughout reflect the substantial influence of factors not consid-

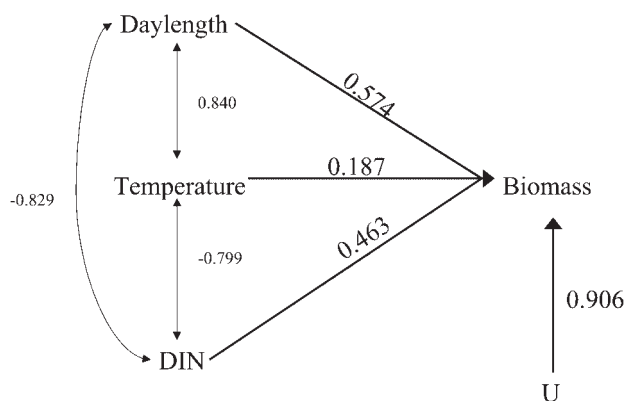


Fig. 4. Path analysis for ulvoid biomass. Daylength, dissolved inorganic nitrogen (DIN) and water temperature when considered together, had a positive effect on biomass. U refers to factors unaccounted for, or error. Values next to single-headed arrows are path coefficients (p). Values next to double-headed arrows are correlation coefficients (r).

ered in this study. While DIN and biomass have a negative correlation coefficient, the path coefficient is positive because of the strong negative correlation of DIN and daylength. To see if differences in DIN between sites resulted in differences in biomass, we regressed mean biomass at each site against mean DIN at each site. This effectively removed variance between sampling dates from the analysis and demonstrated a significant positive relationship between DIN and biomass (Fig. 5). If the PR site is removed from the analysis as an outlier (which is reasonable because its slope, substratum, and dominant plant community is different than all other sites), the coefficient of correlation (r) is 99.3%.

The ulvoid communities around Blakely Island were dominated by *Ulva fenestrata* and *Ulvaria obscura*. Other species were found (i.e., *Enteromorpha linza* (L.) J. Agardh, *E. intestinalis* (L.) Nees, *Ulva cal-*

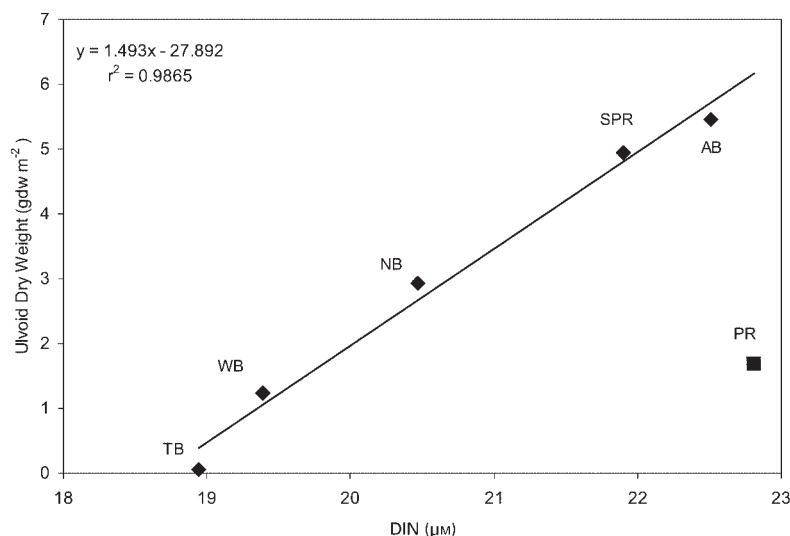


Fig. 5. DIN vs. Biomass. Ulvoid biomass regressed on average dissolved inorganic nitrogen concentrations for each site. The regression equation and r^2 value shown in the Figure exclude the Pinnacle Rock site, which differed from all other sites in having a steeper slope, rockier substratum, and dense kelp growth. If this site is included in the regression analysis, then the regression equation becomes $y = 0.892x - 16.1$ and $r^2 = 0.469$.

Table II. Table of Pearson's correlation coefficients between selected biological, physical, and chemical parameters.

	Biomass	% <i>Ulvaria</i>	DIN	PO ₄ ⁻	Daylength	Surface water temp.	Stable water temp.	Depth	k _z
Biomass	1								
% <i>Ulvaria</i>	0.201	1							
DIN	-0.162 ^B	-0.250	1						
Phosphate	-0.129	-0.238	0.935***	1					
Daylength	0.347***	0.330*	-0.829***	-0.759***	1				
Surface water temp.	0.242**	0.233	-0.870***	-0.743***	0.861***	1			
Stable water temp.	0.299**	0.152	-0.799***	-0.659***	0.840***	0.972***	1		
Depth	-0.014	-0.669***	ND	ND	ND	ND	ND	1	
k _z	0.002	0.330*	-0.602***	-0.437***	0.592*	0.517**	0.413***	ND	1

ND indicates no data in cases where it is not possible to correlate the parameters (e.g., daylength does not vary with depth). *** Correlation is significant at the 0.001 level (2-tailed). ** Correlation is significant at the 0.01 level (2-tailed). * Correlation is significant at the 0.05 level (2-tailed). ^BBorderline case, where $0.05 < p < 0.10$.

ifornica Wille *in* Collins, Holden *et* Setchell, *Ulva stenophylla* Setchell *et* Gardner, and *Ulva taeniata* Setchell *in* Collins, Holden *et* Setchell), but typically accounted for less than 1% of the biomass at any site. For simplicity, the following analyses use the proportion of biomass attributed to *Ulvaria obscura* as an indicator of species composition.

The proportion of biomass attributed to *Ulvaria* varied with depth, site, and date (Fig. 6). Sampling

date \times site \times depth interaction effects were highly significant ($F_{47,269}=2.90$, $p < 0.0005$). Relative *Ulvaria* abundance increased with increasing depth, accounting for 18.6% of the biomass at 0 m, 57.7% at -1 m, and 74.3% at -2 m. Depth alone accounted for 25.6% of the variation in relative *Ulvaria* abundance across depths, sites, and sampling dates (Table II). While most sites had, on average, substantially more *Ulvaria* at -1 m than 0 m, site TB was an exception

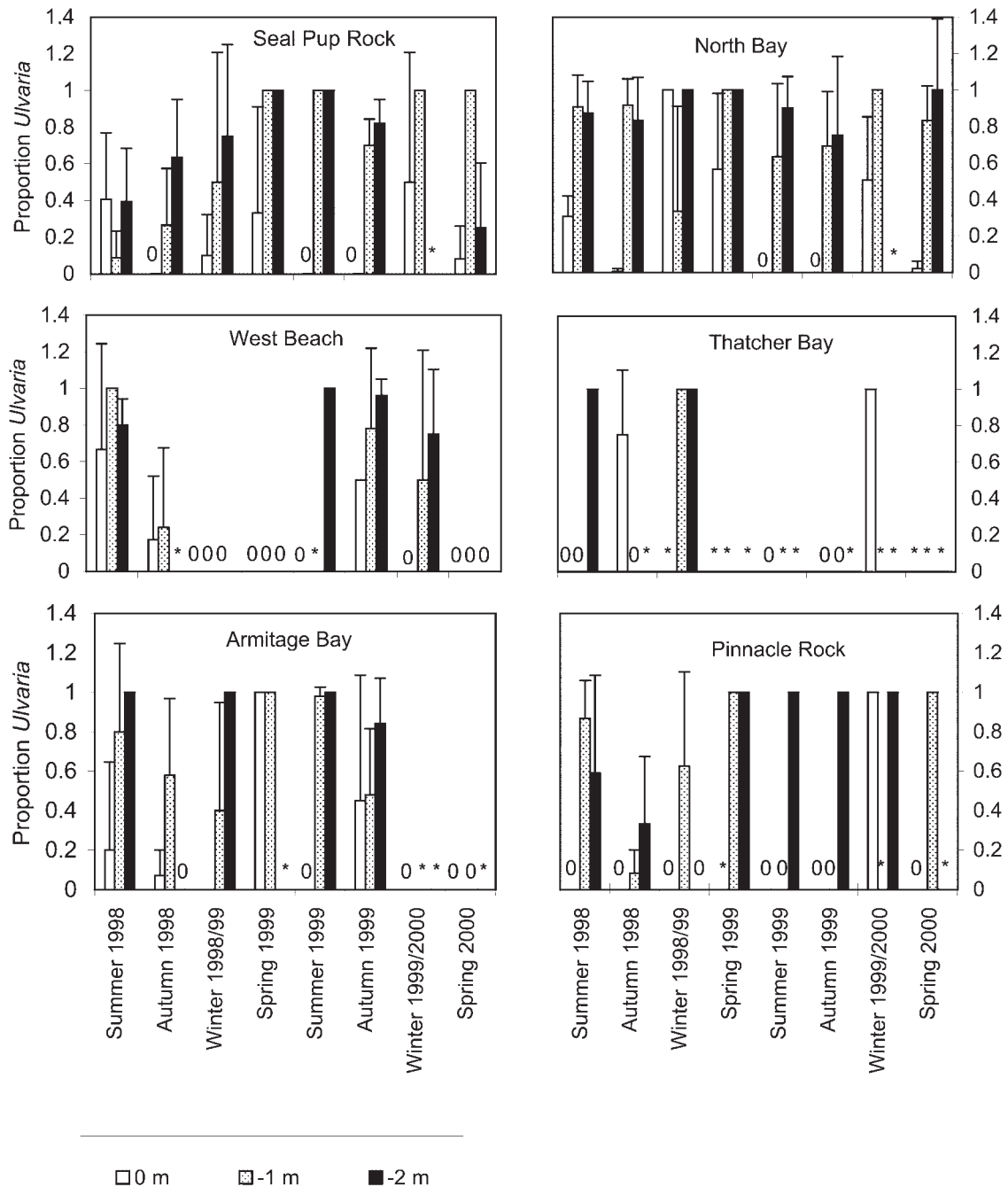


Fig. 6. Proportion of ulvoid biomass attributed to *Ulvaria obscura* at different sites, sampling dates, and tidal elevations. Asterisks (*) in the Figure indicate sampling depths that did not have any ulvoid algae present (i.e., making a calculation of the proportion of biomass attributable to *Ulvaria* impossible), while the numeral 0 indicates depths which had some ulvoid algae present but no *Ulvaria*. Error bars are +1.0 SD.

that did not show a substantial increase in *Ulvaria* shallower than -2 m. PR had the lowest relative *Ulvaria* abundance (32.7%). WB, SPR, TB, and AB had intermediate values (41.2%, 45.5%, 50.0%, and 50.2%, respectively). *Ulvaria* was most dominant (accounting for 58.0% of the biomass) at NB. Differences in the relative abundance of *Ulvaria* between sampling dates did not follow a consistent pattern from year to year when averaged across all depths, but *Ulvaria* was more abundant at 0 m in the winter and in the spring of 1999 than in the summer and fall. Besides depth, the only significant predictor of rela-

tive *Ulvaria* abundance was the coefficient of extinction ($r^2=2.9\%$). *Ulvaria* tended to be more abundant when and where the waters were more turbid, although this only explained a small portion of the variation between quadrats.

Phase III: biomass and species composition at a larger geographic scale

Biomass and species composition varied substantially between sites examined in the second phase of this study (Fig. 7). Sites in the Southwestern Bays and

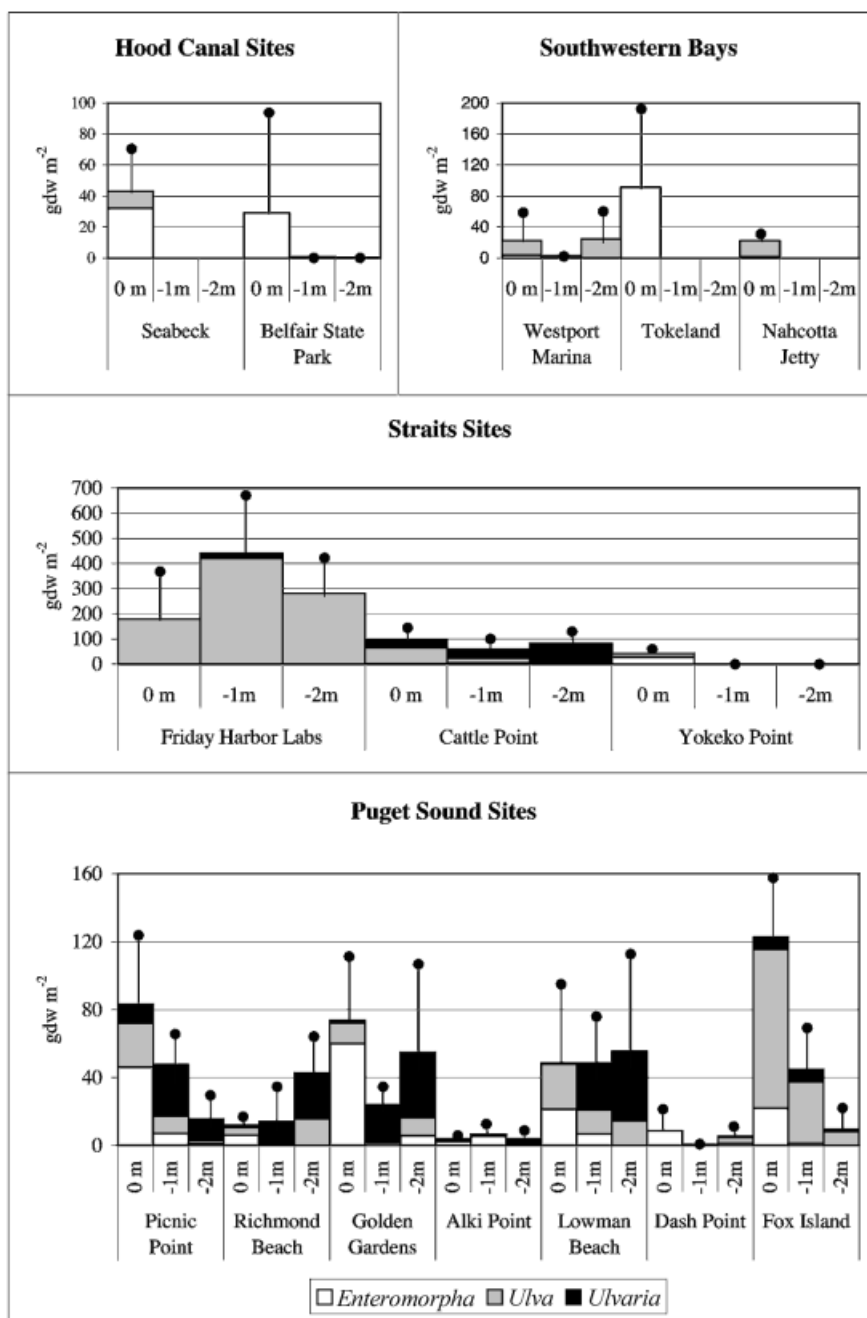


Fig. 7. Phase II sites. Biomass is shown by genus and depth. *Ulvaria* refers to *Ulvaria obscura*. *Ulva* biomass consisted primarily of *Ulva fenestrata*. *Enteromorpha* biomass was distributed among several species, depending on the site examined. Error bars are +1.0 SD.

Hood Canal (WM, TL, NJ, SB, and BSP) had relatively low biomass (from mean \pm 1 s.d. = 7.3 ± 12.7 g dw m^{-2} at NJ to 30.3 ± 52.5 g dw m^{-2} at TL). Three of these sites (TL, NJ, and SB) had no ulvoid algae in the subtidal zone. *Enteromorpha* spp. made up the majority of the biomass at TL (*Enteromorpha prolifera* (O. F. Müller) J. Agardh), SB (primarily *E. prolifera*, but including *E. linza* and *E. intestinalis*), and BSP (primarily *E. prolifera*, but including *E. linza* and *E. intestinalis*). *Ulva fenestrata* was the most abundant species at NJ and WM. *Ulvaria obscura* was completely absent from all 5 of these sites. Ulvoid algal biomass at sites in Puget Sound varied from 4.9 ± 5.1 g dw m^{-2} at DP to 59.2 ± 58.0 g dw m^{-2} at FI. *Enteromorpha* spp. (primarily *E. linza* at these sites, but including *E. prolifera* and *E. intestinalis*) accounted for over half the biomass at 0 m at PP, RB, GG, AP and DP. *Ulvaria obscura* was dominant at -1 and -2 m at PP, RB, GG, AP, and LB. At the sites in the Straits, ulvoid biomass varied from 14.7 ± 24.5 g dw m^{-2} at YP to 300.3 ± 132.1 g dw m^{-2} at FHL. The bloom at FHL was composed almost entirely of *Ulva fenestrata*. At Cattle Point, *U. fenestrata* dominated the intertidal zone while *U. obscura* dominated the subtidal zone. *E. linza* was dominant at YP at 0 m. Very little ulvoid material was found at -1 m and -2 m at YP, probably due to the steep slope and loose substratum at this site.

Discussion

Physical-chemical factors

Thom *et al.* (1988) suggest that nutrient concentrations in Puget Sound are determined by terrestrial and oceanic input. Our observations that nutrient-rich sites in the vicinity of Blakely Island have lower oxygen concentrations, clearer, cooler water, and greater water movement (Kawaky 1999) are more consistent with oceanic upwelling than terrestrial nutrient runoff. Differences in physical chemical parameters between sampling dates were consistent with those reported for the area by other studies (e.g., Thom and Albright 1990, Nelson and Waaland 1997).

Ulvoid biomass

The biomass of bloom-forming ulvoid algae may be controlled by a variety of abiotic and biotic mechanisms, but DIN and light are often thought to be the limiting factors (Duarte 1995, Valiela *et al.* 1997). Increasing ulvoid algal biomass has been associated with increasing seawater [N] in field observations (Valiela *et al.* 1992), mesocosm experiments (Coutinho and Zingmark 1993), field manipulations (Harlin and Thorne-Miller 1981, De Casabianca and Posada 1998), and modeling exercises (Coffaro and Bocci 1997, Bergamasco and Zago 1999). Seasonal changes

in *Ulva* biomass and growth have been directly correlated with DIN by some authors (Rivers and Peckol 1995, Altamirano *et al.* 2000). Others note that DIN does not limit ulvoids when light intensity is low (Rosenberg and Ramus 1982) or at nitrogen-replete locations (De Casabianca and Posada 1998). For example, seawater [N] limited the growth of *Ulva curvata* (Kützing) De Toni only when photosynthesis was light-saturated (i.e., >200 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, Coutinho and Zingmark 1993). In some cases, growth is correlated with DIN, but only during the high-light growing season (Rosenberg and Ramus 1981).

In the present study, different environmental parameters appear to drive annual, geographic, and elevational differences in ulvoid biomass. Marine plant communities in this area are thought to be limited seasonally by light availability (Thom and Albright 1990). Nelson and Waaland (1997) found that modeled light available to seagrasses (at -2.5 m MLLW) near Blakely Island never exceeded 100 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ for over two months in midwinter. The present study notes that biomass peaked in summer and autumn and was best correlated with daylength at sites near Blakely Island.

While light appears to drive annual biomass variation in the present study, DIN may play an important role. DIN, when considered alone, was negatively correlated with biomass. This is caused by the negative correlation between DIN and daylength, which itself has a strong positive correlation with biomass. Path analysis accounts for this negative correlation and shows the underlying positive relationship between DIN and ulvoid biomass once differences in daylength are accounted for. Further, although correlations between various abiotic factors and ulvoid biomass were highly significant, the low coefficient of correlation suggests that other parameters may strongly influence ulvoid biomass. For example, DIN pulses between sampling dates could be important in determining the growth rate of ulvoid algae (Ramus and Venable 1987). Similarly, changes in light availability at different sites, depths, and seasons may not have been adequately represented by daylength and water clarity data alone.

While temperature has been suggested as driving seasonal growth differences in ulvoid algae, the effects of increasing temperature have been found to be positive in some cases (e.g., Duke *et al.* 1989) and negative in others (Rivers and Peckol 1995). In the present study, seasonal differences in temperature are positively correlated with biomass, whether considered independently or as part of a multiparameter path analysis.

Site-to-site differences in biomass appear to be driven by differences in DIN, bathymetry, and exposure to larger water masses. Five of six sites examined on Blakely Island have an extremely strong linear relationship between temporally-averaged DIN and biomass (Fig. 5). Valiela *et al.* (1992) suggest that

short water residence time favors macroalgae over phytoplankton. This is consistent with our observations that extremely enclosed or isolated bays (e.g., Hood Canal Sites, Southwestern Bays Sites, and TB) had very low ulvoid biomass while sites exposed to larger water masses and higher currents had higher biomass. The present study does not consider sites exposed to extremely high water motion (e.g., severe wave action or scouring currents), where ulvoid algae are likely to be detached (Hawes and Smith 1995). Casual observations indicate that ulvoid algae are rare at such sites.

The depth at which maximum ulvoid biomass is found varied from site to site. Within the geographic range considered by this study, substantial accumulations of ulvoid algae have also been noted higher in the intertidal zone than considered here (Price and Hylleberg 1982). These elevational differences in biomass may be caused in part by competition with seagrasses, which would yield a patchy distribution that is uncorrelated with depth. Bathymetry may also play a role. In areas with moderate current, ulvoid algae were found in depressions or level benches that are themselves uncorrelated with depth.

Large differences in ulvoid biomass were noted between sites that were geographically close together. The site with the highest observed biomass on Blakely Island (AB) was flanked by two sites with relatively low biomass (TB and PR). Nelson and Lee (2001) have demonstrated that the ulvoids at site AB limit the extent of an eelgrass (*Zostera marina* L.) meadow. In Washington State (as in many other locales), eelgrass meadows are highly protected ecosystems. Thus within a few kilometers we find sites of high human value with an apparent "green tide" problem and sites that are apparently unaffected. Fine scale monitoring of this phenomenon at multiple tidal elevations may be needed to detect blooms sufficient to harm seagrass ecosystems.

Species composition

Macroalgal blooms are typically reported to be monospecific (Valiela *et al.* 1997), but we observed *Ulva fenestrata* dominating the intertidal zone and *Ulvaria obscura* the subtidal zone at most of the study sites with substantial ulvoid algal biomass. The one notable exception, FHL, lacks *U. obscura* in the subtidal zone. *Ulvaria obscura* dominates the subtidal zone at multiple sites <1 km distant from FHL (T. Nelson and D. Lee, personal observation), however, suggesting that this is an extremely localized phenomenon.

Prior studies of macroalgal biomass in the northeastern Pacific region have rarely noted the importance of *Ulvaria* among ulvoid algal blooms. Vadas (1977) lists *Ulvaria*, (reported as *Monostroma fuscum*) and *Ulva* as members of the shallow subtidal macroalgal community, but does not quantify this ob-

servation. Thom *et al.*'s (1976) and Thom and Albright's (1990) intertidal surveys in central Puget Sound note that *Ulvaria obscura* is a rare, lower intertidal species that accounts for only a small fraction of ulvoid biomass. Price and Hylleberg (1982) suggest that *Ulvaria obscura* (referred to as *M. fuscum*) is a spring ephemeral. This apparent contradiction with the data presented here is readily explained. Prior quantitative studies focused on the intertidal zone, while *Ulvaria* dominates the subtidal zone. Further, *Ulvaria* is less desiccation tolerant than *Ulva* (T. Nelson and A. Nelson, unpublished data). Thus *Ulvaria* may thrive in the low intertidal zone during the spring, but dies off due to desiccation stress as summer progresses. The idea that this species is rare or occurs abundantly only in the spring, however, is refuted by our data. Since *Ulvaria obscura* is circumboreal, its importance may have been underestimated in the Atlantic Ocean as well.

Ecosystem impacts

Anthropogenically-induced macroalgal blooms can overgrow and "suffocate" seagrass meadows and can create anoxic conditions resulting in the loss of diversity and abundance in animal communities (Valiela *et al.* 1997, Tagliapietra *et al.* 1998). Several of the sites examined in this study have sufficient mean algal biomass to reduce eelgrass density (based on biomasses reported to reduce eelgrass density at site AB, Nelson and Lee 2001). During the course of this study we noted several eelgrass meadows with intermediate mean ulvoid biomass but high variance (e.g., WB, NB). These sites lack eelgrass where there are dense patches of ulvoid algae and vice versa. The dense patches of ulvoid algae are probably capable of reducing eelgrass density even though mean ulvoid biomass is not particularly high at these sites.

Ulvoid algal blooms sometimes decline in midsummer, either due to an anoxic crisis (Sfriso *et al.* 1987, Viaroli *et al.* 1996a) or high summer water temperatures (De Casabianca and Posada 1998). Neither anoxia nor a summer decline was noted in this study. Biomass never reached the 1 Kg AFDW associated with such a decline by Viaroli *et al.* (1996b). Rather, reduction in light in the autumn appears to cause the observed reduction in biomass. The bloom at AB was sufficient to create hypoxic conditions at night below the ulvoid mat (< 3 mg/mL at night at 12 °C, T. Nelson, unpublished data), but signs of anoxia were never apparent.

Shifts from seagrass to ulvoid dominated marine plant communities are often associated with increasing nitrogen availability (e.g., Duarte 1995, Taylor *et al.* 1995, Sfriso and Marcomini 1997). Increasing nitrogen availability is likely to increase problematic blooms in the area considered by this study. The sites examined in Phase I, near Blakely Island, although free from substantial or obvious anthropogenic nutri-

ent sources, still have blooms sufficient to negatively impact eelgrass meadows. The strong positive correlation between ulvoid algal biomass and DIN suggests that additional anthropogenic N would increase algal biomass and thus cause greater harm to seagrass meadows.

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