

Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration

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Abstract

On Oregon coastal rocky shores, filter-feeders were relatively abundant and macrophytes were relatively scarce at Strawberry Hill, whereas opposite abundance patterns occurred at Boiler Bay. To determine whether nearshore oceanographic differences were associated with these patterns, we made shore-based measurements of nutrient and Chl *a* concentrations. We used a three-level nested design to identify ecologically appropriate sampling scales: "site" (10s of km), "bench" nested within site (100s of m), and "location" nested within bench (10s of m). Nutrients varied inconsistently but Chl *a* was consistently higher at Strawberry Hill. For Chl *a*, site explained ~70% of the variance, whereas bench and location explained <20%. For nutrients, site and bench explained most of the variance, but neither was consistently more important. The data tentatively suggest that nutrient levels are weakly related to the between-site ecological differences. In addition to the between-site differences, Chl *a* changed seasonally, with maximum levels in summer. For nutrients, temporal changes were more complex, with highest levels tending to occur in late summer and autumn. No nutrient, however, was scarce enough at either site to limit phytoplankton growth, with the possible exception of nitrate in June. These results were consistent with the hypothesis that nearshore phytoplankton standing stock, a bottom-up factor, could underlie differences in rocky intertidal community structure.

Despite the obvious juxtaposition of coastal planktonic and nearshore benthic habitats, marine scientists working in these environments have proceeded largely independently. In recent years, however, the likelihood that these habitats are often tightly linked biologically has led to heightened awareness of the need for better integration of these subdisciplines (e.g. Witman et al. 1993; Gaines and Bertness 1994; Menge 1992). For example, larval transport processes in the nearshore water column can have important consequences for benthic intertidal and subtidal populations (Ebert and Russell 1988; Gaines and Roughgarden 1985; Shanks 1995). Other evidence suggests that benthic and pelagic habitats may be tightly linked through nutrient and trophic pathways (e.g. Bertness et al. 1991; Duggins et al. 1989; Thresher et al. 1992).

Determining the causes of spatial and temporal variation in the structure of communities is a central issue in com-

munity ecology (e.g. Hairston 1989; Menge and Sutherland 1987; Menge and Olson 1990). In marine intertidal habitats, ecologists have gained insight into causes of variation at local scales, ranging generally from 10s of centimeters to 100s of meters (e.g. *see* Menge and Farrell 1989; Paine 1994). Controlling processes emphasized generally include physical factors (wave exposure, stress from heat, and desiccation) and biotic factors (predation, grazing, competition, commensalism, and mutualism), although recent studies (Asmus and Asmus 1991; Williamson and Rees 1995) have suggested that small-scale (centimeters to meters) nutrient variations from animal excretion can have important effects on algal growth. At scales roughly ≥ 1 km, however, far beyond the scales of most field experiments (usually centimeters to 10s of meters), community variation remains largely unexplained (e.g. Foster 1990; Menge 1992; Menge et al. 1994). Determining the causes of such large-scale differences represents one of the current major challenges in ecology. As implied above, obvious potential sources of such patterns include variation in both oceanographic transport and productivity in coastal waters.

To evaluate the importance of coastal processes as a factor underlying unexplained variation in the structure and dynamics of rocky intertidal communities, we initiated a four-part study to evaluate the nature and strength of the link between nearshore benthic and pelagic communities. The first part, and the subject of this paper, was to quantify nutrients and Chl *a* at two sites contrasting in community structure. Our goal was to determine whether between-site differences were consistent with a hypothesis of spatially and temporally persistent differences in magnitude of a benthic–pelagic link. The other parts of the study (to be reported elsewhere) were,

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Table 1. Contrasting patterns of space occupancy in the low zone at Boiler Bay (BB) and Strawberry Hill (SH). Data are mean \pm 1 SE with $n = 10$ (BB 1981, SH 1989, 1990) or 15 (BB 1983, SH 1982) 0.25-m² quadrats per transect per year per site.

	Boiler Bay		Strawberry Hill		
	1981	1983	1982	1989	1990
Sessile invertebrates*	4.8 \pm 1.0	2.5 \pm 0.8	42.7 \pm 7.7	52.7 \pm 13.5	43.2 \pm 6.0
Algal understory†	65.1 \pm 7.2	77.8 \pm 6.3	75.8 \pm 6.0	16.9 \pm 2.9	29.3 \pm 4.2
Algal canopy‡	73.2 \pm 9.3	71.0 \pm 10.3	51.7 \pm 9.4	6.0 \pm 3.8	7.3 \pm 2.2
Bare/algal crusts§	39.3 \pm 5.1	36.1 \pm 4.1	29.2 \pm 3.1	30.5 \pm 5.7	28.6 \pm 6.7

* Includes barnacles, mussels, sponges, tunicates, anemones, bryozoans, hydrozoans, and polychaetes.

† Includes algal turfs, foliose algae, bladed algae, and surfgrass <15-cm blade length.

‡ Includes kelps and surfgrasses >15-cm blade length.

§ Includes bare rock, under urchins and chitons, dead algal crust, sand, coralline crusts, and fleshy crusts.

for the same two sites (assuming part 1 revealed differences), a long-term, in-depth study of nearshore oceanographic conditions [nutrients, Chl *a*, particulate organic matter (POM), dissolved organic matter (DOM), temperature, transport], as well as experimental analyses of interspecific interactions, growth rates of filter-feeders and seaweeds, and recruitment rates; and at multiple sites, a study of nutrients, Chl *a*, filter-feeder growth rates, temperature, and recruitment in relation to community pattern.

Variation in benthic community structure

Community structure of the low rocky intertidal zone at Boiler Bay (BB) on the central coast of Oregon contrasts with that at Strawberry Hill (SH), 80 km to the south (Menge 1992; Menge et al. 1994; Table 1). Relative to BB, at SH sessile invertebrate abundance was high and seaweed abundance was low (Table 1).

Mobile invertebrates (limpets, chitons, seastars, whelks) were also more abundant at SH. At wave-exposed sites, for instance, herbivore densities at SH were nearly 5 \times those at BB (overall means \pm 1 SE of four transects/site: 90.5 \pm 31.3 vs. 19.1 \pm 5.0; No. 0.25 m⁻²). Similarly, seastar densities at SH were nearly 7 \times those at BB (means \pm 1 SE m⁻² of four plots/site: 5.6 \pm 0.3 vs. 0.8 \pm 0.1; plot area range, 33–163 m²; see Menge et al. 1994). Although quantitative sampling of community pattern has been irregular (Table 1), more than a decade of study and observation suggests that these patterns are both persistent through time and representative of the respective regions within a few kilometers of each site. Furthermore, observations made at 15–20 other sites along the Oregon coast suggest these contrasting patterns are representative of the range of variation on these shores.

Experiments carried out simultaneously at both sites indicated that community dynamics differed as well. Specifically, the intensity of predation by seastars on mussels, growth rates of barnacles and mussels, and recruitment densities of mussels were all low at BB and high at SH (Menge 1992; Menge et al. 1994; Navarrete and Menge 1996). Again, long-term field observations suggested that these differences were representative of substantial stretches of shoreline in the region of each site.

Several lines of evidence suggested that between-site differences in both transport processes and nearshore oceanographic

conditions (phytoplankton productivity, particulates, nutrients) could underlie the ecological differences between the two sites. In particular, the higher growth rates of two groups of filter-feeding invertebrates, mussels and barnacles (Menge 1992; Menge et al. 1994), indicated that the availability of planktonic food (phytoplankton, particulate material) might be higher at SH. The contrasting seaweed abundances suggested that, among other things, nutrients might also differ between sites. For example, the higher algal abundance at BB could result from higher nutrients at BB, as suggested for Año Nuevo Island in California, a site of high nitrogen input from marine mammals (Hansen 1981). Furthermore, higher mussel recruitment rates at SH (Menge et al. 1994) suggest that larval transport, survival, or both might also differ between sites.

General oceanographic conditions

Oceanographic variation in the coastal region may explain some of the differences between these communities. The Oregon coastal system is strongly influenced by the southward-flowing California current (Huyer et al. 1978). Hydrographic conditions vary seasonally, with winter and summer conditions separated by relatively brief transitional periods in spring and autumn (Strub et al. 1987b; Strub and James 1988). In winter, winds are primarily onshore from the west and southwest. Currents tend to flow northward and onshore near the surface and vary with depth (Huyer 1977; Huyer et al. 1975; Strub et al. 1987a). In summer, winds are predominantly northwesterly but variable, alternating between those producing coastal upwelling (northwesterlies) and upwelling relaxations (westerlies to southwesterlies) (Huyer 1983). Northwesterly winds enhance the rates of southward flow of the California current and increase the offshore flow of surface waters, thereby producing upwelling. During relaxations, winds vary in strength and direction, reducing or even reversing the direction of flow of surface currents to onshore and/or northward (Huyer et al. 1975; Send et al. 1987; Stevenson et al. 1974).

Summer coastal upwelling produces high levels of primary production in surface waters (e.g. Smith 1974, 1981, 1995). Surface pigment concentrations in satellite images from 3 to 25 km offshore show a maximum in July and minimum in winter (Strub et al. 1990). From 0 to 3 km (here

termed "nearshore"), satellite imagery is ineffective and sampling from oceanographic vessels is hazardous. As a result, little quantitative information is available on nearshore oceanographic conditions.

Here we present results of a sampling program initiated to determine whether between-site differences in nearshore oceanographic conditions existed between BB and SH. By means of a nested sampling design, we quantified levels of nutrients and Chl *a* in the waters bathing each shore. Measurements of these relatively easily quantified characteristics also provided the first step in determining whether conditions favorable to bottom-up differences (e.g. Carpenter 1988; McQueen et al. 1989; Menge 1992), both in algal growth and planktonic food availability for filter-feeding invertebrates, existed at the sites.

As implied by earlier summaries indicating higher growth rates of filter-feeders and higher mussel recruitment rates, we expected to find higher levels of Chl *a* (a measure of phytoplankton abundance) at SH than at BB. For nutrients, there were three possibilities. Our primary expectation was that higher concentrations of phytoplankton at SH could result from higher nutrient levels at this site. The reverse of this—that nutrients were higher at BB and supported the higher abundance there of seaweeds—was considered the second most likely alternative. Because we expected differences, we considered a no-difference alternative as least likely.

With respect to spatial scale, we expected the largest differences in both factors to occur at the scale of site (10s of km), with possible occasional differences at the bench-within-site scale (100s of m) and no difference at the location-within-bench scale (10s of m). As indicated below, variation was significant mostly at large (site; both Chl *a* and nutrients) but also at intermediate (bench within site; primarily nutrients) spatial scales. Between-site differences persisted in phytoplankton abundance but nutrient differences were not persistent, at least on monthly timescales. Results were thus consistent with the hypothesis that at least some aspects of large-scale differences in benthic community structure and dynamics were linked to nearshore oceanographic variation.

Methods

Study sites—Detailed descriptions of the study sites are available elsewhere (e.g. Menge et al. 1994; D'Antonio 1986; Turner 1985). Briefly, both sites include broad rocky benches with a range of wave exposures. These intertidal communities are typical of rocky shore assemblages in the Pacific Northwest, with the exceptions of the differences in relative dominances of seaweeds, sessile invertebrates, and invertebrate consumers summarized above. Tides are mixed semidiurnally, and tidal excursion ranges from ~ -0.76 m to $+2.93$ m, where 0 m is the long-term average of mean lower low water (MLLW). Sea-surface temperature nearshore ranges between ~ 7 and 14°C .

Sampling design—With the notable exception of some South African studies (e.g. Bustamante et al. 1995a,b), little effort has been made to determine the association between

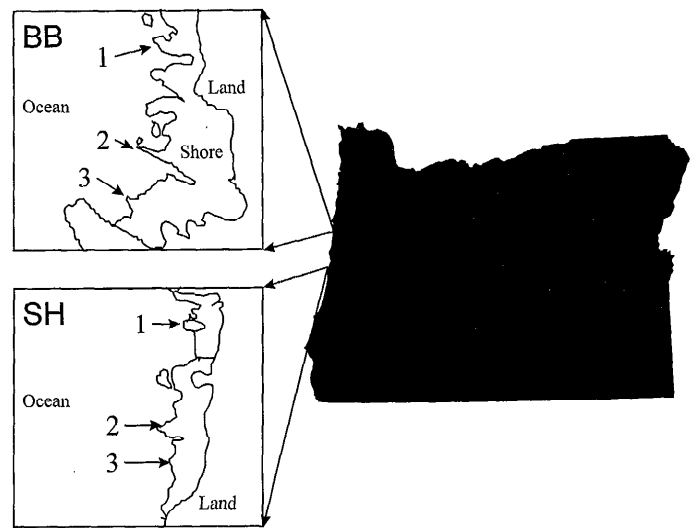


Fig. 1. Diagrams showing shorelines at Boiler Bay (BB) and Strawberry Hill (SH) as located on the central Oregon coast, including locations of benches where water samples were taken. Linear vertical dimension of each diagram is ~ 1.5 km.

nearshore oceanographic conditions and rocky intertidal community structure and regulation. We thus devised a sampling scheme that we thought would reliably capture the patterns of variation in nutrients and Chl *a* in space and time. Both BB and SH include several rocky benches with similar communities along stretches of shoreline ~ 1.5 km long. At each site, we selected three benches (numbered 1–3 from north to south; the middle benches were our main sites earlier—Menge 1992; Menge et al. 1994, 1995), spanning a range of ~ 1 km (Fig. 1). On the basis of the spatial extent of coastal summer phytoplankton blooms often visible from shore (extending ~ 1 km offshore and up to 10s of km alongshore), as well as the results of our previous field studies of biotic interactions (Menge et al. 1994), it seemed that a within-site sampling scheme covering a maximum range of ~ 1 km would adequately represent relevant scales at the level of site.

The sampling locations at BB ($44^{\circ}50'N$, $124^{\circ}03'W$; Fig. 1) were bounded to the north by Fogarty Creek Point, a site also used extensively for ecological research. The southern boundary at BB is Government Point, beyond which the rocky shores of Depoe Bay and Cape Foulweather continue for some 10 km. The beach complex at SH ($44^{\circ}15'N$, $124^{\circ}07'W$; Fig. 1) consists of a series of rocky benches and sandy beaches and is part of a 10–15-km stretch of similar shoreline spanning centrally located Cape Perpetua.

To evaluate the scales of significant variation in nutrients and Chl *a* in two-dimensional space, we initially sampled at a range including scales smaller than those for which we expected to find meaningful variation. Three locations were selected within each of the three benches at each site; within each location we collected samples from three plots. This established a sampling design at four nested spatial scales: plots, 1–2 m apart; locations, 10–20 m apart; benches, 100–500 m apart; and sites, ~ 80 km apart. In February and March 1993, for measurements of Chl *a* and four nutrients

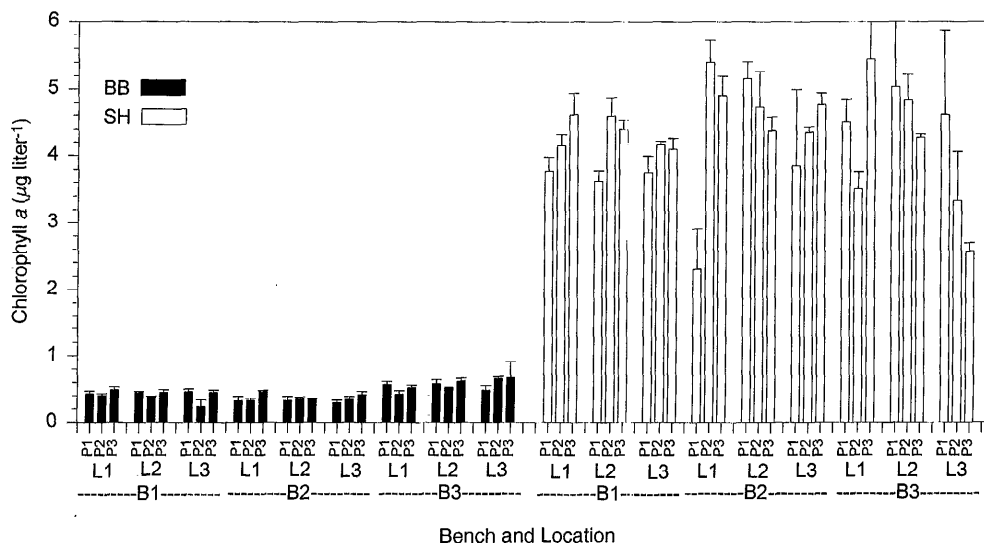


Fig. 2. Results of sampling scale analysis for Chl *a* in March 1993. Bars represent means for three bottles; error bars in this and all subsequent figures are ± 1 SE of the mean. Labels for abscissa represent nested sampling design: B1, B2, B3—benches 1–3; L1, L2, L3—locations 1–3; P1, P2, P3—plots (replicates) 1–3. Site was significant at $P < 0.001$; other factors were not significant (see Table 2).

[NO₃⁻, NO₂⁻, PO₄³⁻, and Si(OH)₄], we collected three 250-ml water samples (subsamples) per plot, producing a total of 182 samples. After these samples had established that there was little or no variability at the 1–2-m scale [$P_{\text{plot(location)}} \gg 0.05$], replicate samples were collected at each location (scale of 10–20 m).

In this part of the study, we did not collect replicate samples at the level of site, primarily because our aims were to determine whether there were ecologically meaningful differences between sites and, if so, what within-site sampling scale and level of replication were adequate to accurately represent nutrient and particulate concentrations at the site level. Later multisite sampling suggests that nearshore patterns observed at BB and SH are representative of lengthy (100+ km) sectors of the Oregon coast (B. Menge et al. unpubl. data).

Sampling protocol—In February 1993, water samples were collected by filling opaque plastic (HDPE) brown bottles at the waters' edge. Thereafter, samples were collected by clamping bottles to the end of a 3-m-long pole and dipping the bottles into the water from the shore. In all cases, we plunged the bottles (250 ml for Chl *a* and nutrients) to a depth 20–40 cm below the surface. After collection, samples were placed on ice in coolers and returned, usually within 30 min, to the laboratory for processing.

Laboratory processing followed established techniques (Parsons et al. 1984). We passed 50-ml samples from each 250-ml bottle through 25-mm combusted Whatman glass-fiber filters (GF/F) with pore size of 0.7 μm . The filtrate was then frozen in HDPE bottles for later analysis of nutrients in a Technicon autoanalyzer. For estimates of Chl *a*, 100 ml was then filtered under low vacuum pressure (≤ 180 mm Hg) through a second Whatman GF/F filter. Chl *a* concentration

was determined with a Turner Designs 10 fluorometer after extraction in 90% HPLC acetone for 12 h in the dark at -20°C . Prior calibration of the fluorometer was done with a pure Chl *a* standard purchased from Sigma Chemical Co. Finally, nitrate, nitrite, phosphate, and silicate were quantified by standard autoanalyzer techniques (Atlas et al. 1971).

Data analysis—Because the sampling design was nested (plot within location, location within bench, bench within site) and samples were considered random, monthly data were analyzed with nested ANOVA (Chl *a*) or nested MANOVA (nutrients) (Sokal and Rohlf 1995). Site was considered a fixed effect (because we were interested in contrasting specific sites that we knew differed in at least some respects), whereas bench, location, and plot were random, so the analyses were mixed-model nested ANOVAs (Sokal and Rohlf 1995). The ANOVA assumption of normality of residuals was checked by visually examining normal probability plots. Similarly, equality of error terms were visually evaluated by examining plots of estimated values against residuals.

Results

Spatial sampling scale—The sampling scale study suggested that in March, significant spatial variation in Chl *a* existed only at the largest spatial scale (i.e. site; Fig. 2, Table 2). Site accounted for 93.6% of the total variance in this dataset (Table 2). Variation observed at the levels of plot, location, and point was statistically insignificant, accounting for $<0.4\%$ of total variance (Table 2). Chl *a* concentration was ~ 8 times greater at SH than at BB.

Results of the sampling scale study for nutrients were mixed. Neither nitrate nor phosphate displayed significant

Table 2. Evaluation of the effects of site, point, location, and plot on level of Chl *a* [$\log(\mu\text{g Chl } a \text{ liter}^{-1})$] in March 1993. The analysis was a nested ANOVA, with bench nested within site, location nested within bench, and plot nested within location. Three replicate samples were collected at the plot scale. In each analysis, each effect above plot (site, bench, location) was tested by using the mean square of the next lowest factor as the error term [e.g. the effect of site was tested with the MS for bench (site) with 1,4 df]. Probability in boldface was significant at $P < 0.05$.

Source of variation	df	MS	F	P	R ²
Site	1	65.667	864.0	0.000008	93.6
Bench (site)	4	0.076	2.10	0.20	0.4
Location (bench)	6	0.036	0.79	0.61	0.3
Plot (location)	6	0.046	1.75	0.11	0.4
Error	143	0.0261			5.3

between-site differences ($P = 0.93, 0.19$, respectively; 1,4 df). Furthermore, whereas differences among locations ($P = 0.003$; 6,6 df) and plots ($P = 0.0013$; 6,143 df) were significant for nitrate and differences among benches ($P = 0.038$; 4,6 df) were significant for phosphate, these contributed a maximum of only $\sim 28\%$ of the total variance in each case. Examination of the data (Fig. 3A,B) suggests that these statistically significant differences are not very important.

In contrast, for silicate, site contributed the greatest proportion of total variance (78.7%; $P = 0.015$; 1,4 df), and SH

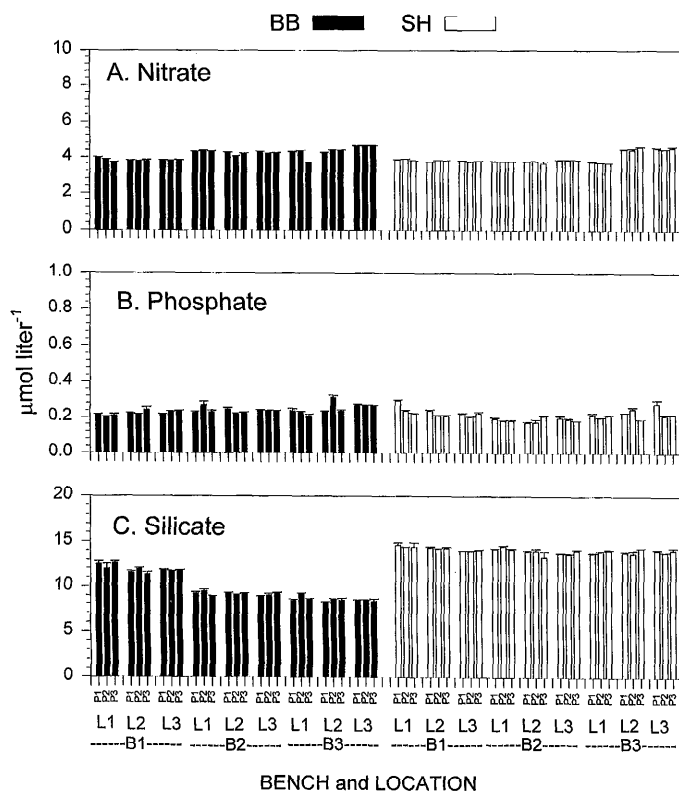


Fig. 3. Results of sampling scale analysis for three nutrients in February 1993. Additional explanation given in legend to Fig. 2 and Table 2.

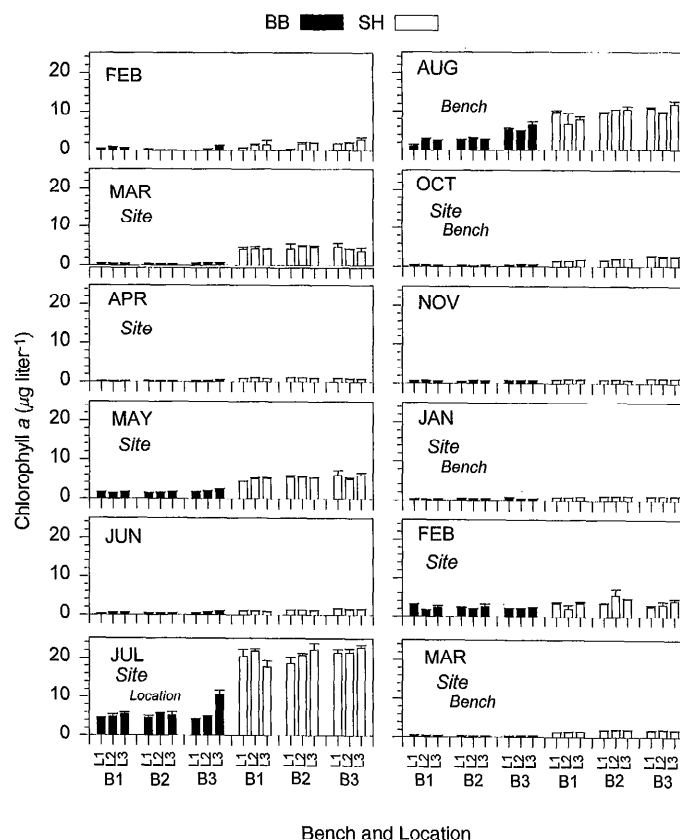


Fig. 4. Monthly levels of Chl *a* from February 1993 to March 1994 by site (BB, SH), bench, and location. Months with significant differences at one or more sampling scales are shown by including "site," "bench," or "location" in the panel for that month. Data analysis used nested ANOVA as in Table 2. Because monthly values were not independent, probability levels were Bonferroni adjusted [$P = (0.05/12 \text{ tests})$ or 0.0042] to reduce the buildup of type 1 error. No samples could be taken in September and December. Abscissa labeling code as in Fig. 2.

had strikingly higher levels than did BB (Fig. 3C). Differences among benches within sites ($P = 0.00004$; 4,6 df) and locations within benches ($P = 0.003$; 6,6 df) were also statistically significant; however, only between-bench differences contributed substantially to total variance (19.1%). Although the nested-design ANOVA could not evaluate statistical interactions between scales, it seems as if silicate varied more among benches at BB than at SH (Fig. 3C).

These results suggest that to successfully represent spatial variation in Chl *a* and silicate (at least), a sampling scheme at the levels of site and bench within site is necessary. Although statistically significant variation was observed down to the scale of plot within location (for nitrate), samples at this spatial scale accounted for a maximum of only 2% of total variance. The smallest scale accounting for a substantial proportion of variance (28%; nitrate) was location within bench, so samples after March 1993 were taken at three spatial scales: site, bench within site, and location within bench.

Monthly changes—Chl *a* levels varied significantly but differentially with site, bench, and location (Fig. 4). Within

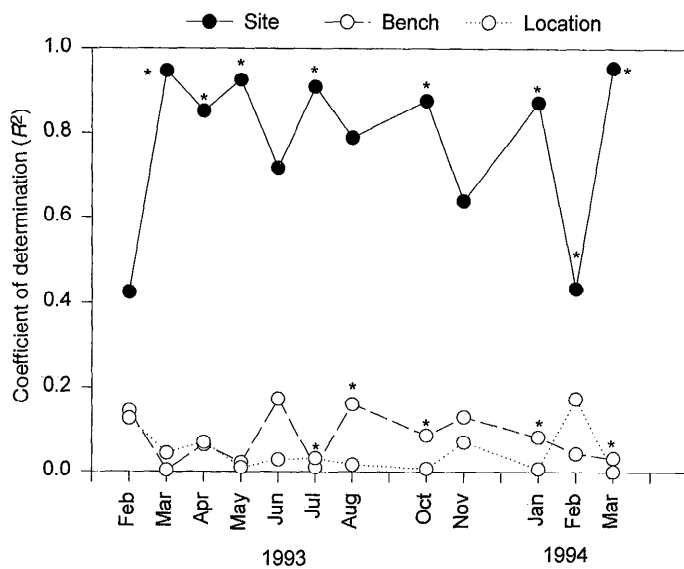


Fig. 5. Proportion of total variance, as represented by the coefficient of determination (R^2), in Chl *a* levels in each month explained by site, bench, and location. Asterisks indicate months and scales with significant differences. Further explanation given in text.

sites, significant variation at the scale of bench was observed in August and October 1993 and January and March 1994; at the scale of location within bench, significant variation was observed only once, in July 1993. Variation between sites, however, had by far the largest difference (in 8 of 12 months sampled, Chl *a* was significantly greater at SH; Fig. 4). This between-site difference is even more clearly demonstrated by examining the variance explained by the analyses when partitioned among sites, benches, and locations (Fig. 5). Site invariably explained the greatest proportion (43% at minimum; generally in the 80–90% range) of total variance, with bench and then location generally explaining small amounts of variance (18% at maximum; Fig. 5). Overall, sampling at the scales of bench and site captures most of the variability in Chl *a*. Furthermore, samples within a single bench adequately reflect the between-site differences seen here.

Nutrient variation in space and time was more complex than was Chl *a* variation, with significant differences observed most often at the bench scale, less often at the site scale, and infrequently at the location scale. Nitrate tended to be higher from July to January and lower in spring, spanning a range of nearly two orders of magnitude (~ 0.2 – $18 \mu\text{mol liter}^{-1}$; Fig. 6).

Nitrate varied with site only twice in the 10 monthly samples taken—in August 1993 (higher at SH) and in February 1994 (higher at BB) (Fig. 6). Differences at the bench scale occurred in 6 of 10 months, all in the warmer months (May–October) except for February 1994. Variations at the location scale were in February, April, and June 1993. Inspection of the data (Fig. 6), however, suggests that the greatest differences were in July (bench) and August (site); the other significant differences are barely noticeable.

Nitrite (data not shown) was always low (range, 0.03–0.7

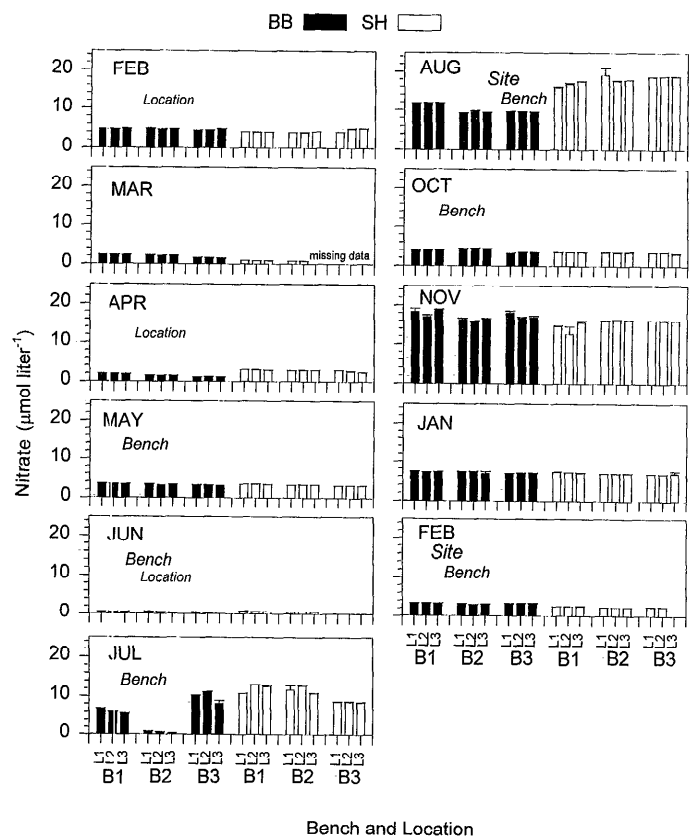


Fig. 6. Monthly levels of nitrate from February 1993 to February 1994 by site, bench, and location. Analysis for nutrients (nitrate, phosphate, silicate) employed nested multivariate ANOVA, with Bonferroni-adjusted P values used in the univariate comparisons. Additional explanation in legend to Fig. 4.

$\mu\text{mol liter}^{-1}$) relative to nitrate (range, 0.3– $19 \mu\text{mol liter}^{-1}$; Fig. 6). We assume that in this generally nutrient-rich environment, statistically significant variation in this nutrient (differences were seen among benches in March, April, August, and October 1993 and between sites in January and February 1994) is ecologically insignificant.

For phosphate, site differences were observed only once in 11 sampled months (in January 1994, BB > SH; Fig. 7). Variation among benches occurred in 5 of 11 months (April, May, July, August, and October), but differences among locations were never significant. Concentrations of phosphate were higher from August through November, but even the lowest concentrations observed (0.3 – $0.4 \mu\text{mol liter}^{-1}$ in June) were high relative to phytoplankton requirements for growth (Tilman and Kilham 1976).

Silicate exhibited between-site variation more frequently than did the other three nutrients, differing in 6 of 11 months (February, March, April, August 1993 and January and February 1994; Fig. 8). When levels differed, silicate was invariably higher at SH (Fig. 8). Similarly, silicate varied significantly at the bench scale in 7 of 11 months (February, March, May, June, July, August, and November) but never varied at the location scale. Although the range of silicate levels was less than an order of magnitude (~ 3 – $23 \mu\text{mol}$

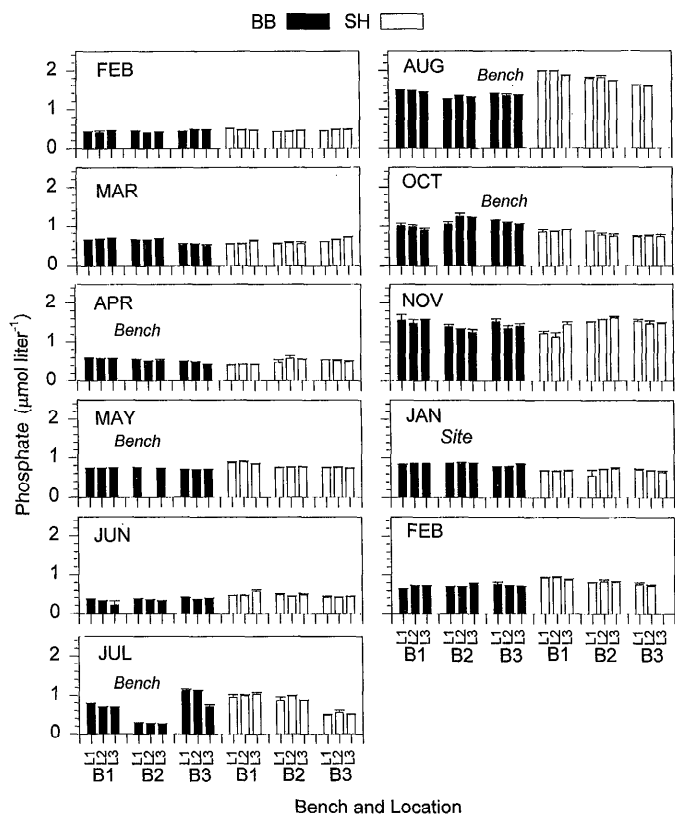


Fig. 7. Monthly levels of phosphate from February 1993 to February 1994 by site, bench, and location. Additional explanation given in legends to Figs. 4 and 6.

liter⁻¹), absolute levels were often relatively high and unlikely to have any direct effect on phytoplankton productivity (Thomas and Dodson 1975). Thus, in contrast to Chl *a*, nutrient differences were less consistent both spatially and temporally. For silicate, however, when there were between-site differences (5 of 11 months), BB < SH.

Examination of variance partitioned by scale documents this spatially and temporally lower consistency in nutrients (Fig. 9). Unlike the situation with Chl *a*, where variation was mostly due to site differences (with SH > BB), nutrients exhibited large and often statistically significant variation at both site (both SH > BB and BB > SH) and bench (but not location) scales. Evidently, nutrients can vary substantially at distances of only 100s of m. Moreover, the data (Figs. 6–8) indicate that variation at the 100-m scale shifts haphazardly among benches; through time, no bench consistently had higher or lower levels.

Discussion

From February 1993 to February 1994, abundance of phytoplankton, as indexed by Chl *a* concentration, was consistently and usually significantly greater at SH than at BB. Furthermore, although Chl *a* often varied significantly at the two larger spatial scales (site and bench), site consistently accounted for most of the variance (Fig. 5). Nutrients also differed between sites and among benches, but such differ-

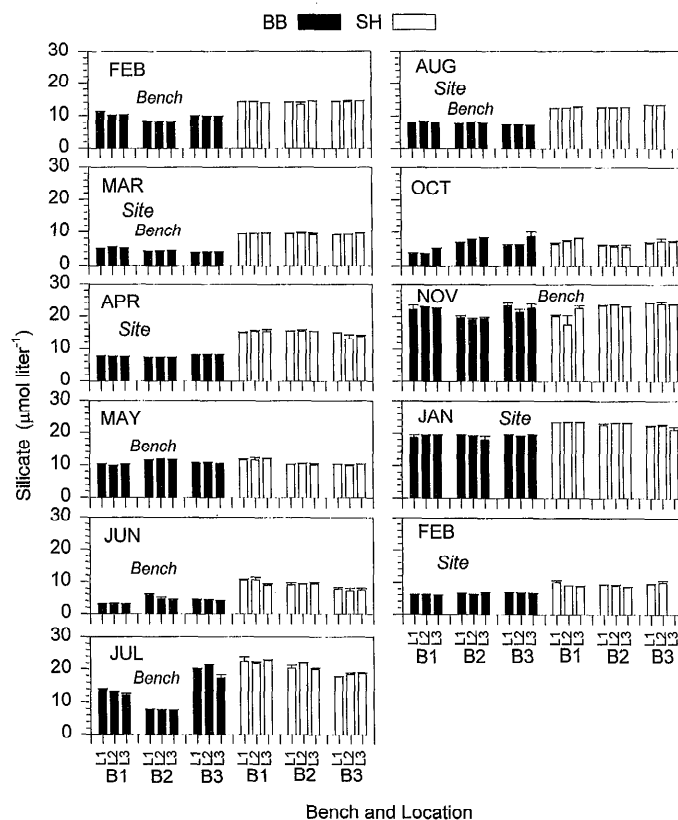


Fig. 8. Monthly levels of silicate from February 1993 to February 1994 by site, bench, and location. Additional explanation given in legends to Figs. 4 and 6.

ences were less consistent spatially and temporally, with site and bench scales alternating in their relative importance (Fig. 9). Because nutrient differences between sites were less consistent, and within-site differences were often greater than between-site differences, support for our first expectation for nutrients—that higher concentrations of nutrients supported higher Chl *a* concentrations (*see introduction*)—is weak. Note also that such irregular patterns in nutrients, as well as the weak tendency for silicate to be higher at SH, are not consistent with the second alternative, that higher nutrients at BB might explain the higher seaweed abundance at this site.

These considerations suggest the tentative conclusion that nutrients do not explain between-site differences in community structure. Several points warrant caution in advancing this notion, however. For between-site differences in silicate, concentrations at BB were lower than at SH. During the upwelling season (April–August), although differences were only sometimes statistically significant, BB tended to have lower average concentrations of nitrate and silicate than did SH (Figs. 6, 8). Appropriate temporal sampling scales for nutrients are very likely much less than monthly, since concentrations can change dramatically within a few days (e.g. Fujita et al. 1989; B. Menge et al. unpubl. data). This latter point, combined with the apparent greater patchiness of nutrients vs. Chl *a* (as suggested by the tendencies for nutrients to most often vary significantly at the smaller

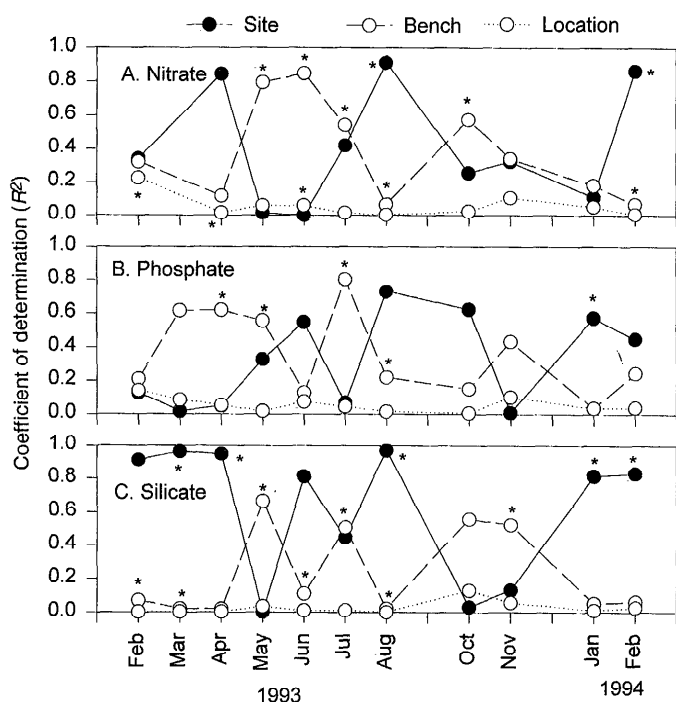


Fig. 9. Proportion of total variance, as represented by the coefficient of determination (R^2), in concentrations of nitrate, phosphate, and silicate in each month explained by site, bench, and location. Asterisks indicate months and scales with significant differences. Further explanation given in text.

bench scale and for Chl *a* to most often vary significantly at the larger site scale; Figs. 4, 6–8), indicates that the role of nutrients may not be fully resolved. We will address this issue elsewhere.

Although SH had consistently higher levels of Chl *a*, both sites varied in parallel in both nutrients and Chl *a* (Figs. 4, 6–8). These data thus suggest that, as previously observed farther offshore (Strub et al. 1990), monthly and seasonal changes in these factors are also a general coastal phenomenon in the nearshore, occurring at latitudinal scales of ≥ 100 km. Our discovery that variation at the scale of 10s of km can occur within this broad pattern has considerable ecological significance, although further research is needed to explore its general importance.

The causes of such coastal oceanographic change, including summer upwelling, are reasonably well known (Huyer et al. 1978; Smith 1981). The causes of the new variation documented here (at scales of 10s of km) remain unknown at present, although any of several alternatives, including localized upwelling hotspots and shore or bottom topography or composition (e.g., MacLachlan 1990; Bustamante et al. 1995a,b), are possible. The most obvious features associated with the difference between BB and SH are that SH occurs along a shoreline consisting of rocky reefs punctuated by sandy beaches, with seasonal influxes of sand in sheltered areas, whereas BB occurs along a predominantly rocky shoreline with no sand influxes (e.g. D'Antonio 1986), and the shelf to the 100-m isobath off SH is broader than at BB (10 km vs. 4.5 km). MacLachlan (1990) has suggested that

wave-beaten sandy beaches are highly productive, presumably owing to frequent resuspension of nutrients and diatoms by wave turbulence and perhaps also to release of silicate by weathering of sand particles (see Hecky and Kilham 1988). It is thus possible that higher phytoplankton concentrations at SH reflect the influence of nearby sandy beaches. A broader shelf off SH may influence nearshore productivity by altering water-exchange rates alongshore. Elsewhere we suggest that water movement in the offshore direction during upwelling relaxations is slower at SH than at BB (B. Menge et al. in prep.), or, alternatively, more strongly onshore at SH during upwelling relaxations (Peterson et al. 1988). Either possibility could lead to higher accumulation of nearshore phytoplankton populations at SH than at BB. Testing these and other possible alternatives will depend on future physical and biological oceanographic research in the nearshore environment.

To sample nutrients and Chl *a* in nearshore waters, we think that a scheme with sampling at 100s of m nested within 10s of km provides the most relevant scales. As noted earlier, however, the amount of variability displayed at the bench scale for Chl *a* (at least) was small compared to the site scale. This finding suggests that even samples at single benches separated by several kilometers are likely to reasonably accurately quantify the variability that exists among sites. Nutrients appear to vary far more than does Chl *a* at the intermediate (100s of m) spatial scale, and adequate sampling of nutrients should probably incorporate this scale.

We initially anticipated that during some months, nutrients might limit primary production of phytoplankton and thereby influence productivity at the two sites. Our results, however, show that nutrients almost always exceed levels known to limit phytoplankton growth. The half-saturation constant (the concentration at which growth is half the maximum growth rate) for coastal phytoplankton is $0.012\text{--}0.05 \mu\text{M}$ for phosphate (Tilman and Kilham 1976). The minimum phosphate concentration during our monthly sampling was $0.35 \mu\text{M}$, which is well above the requirement for sufficient phytoplankton growth. Similarly, for silicate the half-saturation constant for phytoplankton growth is $0.33\text{--}0.75 \mu\text{M}$ (Thomas and Dodson 1975). The minimum silicate observed during our monthly sampling was $4.5 \mu\text{M}$. High silicate concentrations may contribute to the abundance of diatoms at both sites. The half-saturation constant for nitrate-limited growth is $0.1\text{--}1.9 \mu\text{M}$ (Carpenter and Guillard 1971). Because nitrate concentrations were within this range at times during spring, nitrogen-limited growth is possible at both sites. However, our nutrient data suggest that periods of low nutrient concentrations were infrequent during this 13-month period, and we conclude that at least during this sampling period, phytoplankton growth was not nutrient limited at either site.

The Chl *a* data presented here are consistent with a bottom-up hypothesis to explain differences between intertidal communities at BB and SH. If higher levels of Chl *a* (microscopic examinations indicate the primary phytoplankters were three diatom genera, *Nitzschia*, *Skeletonema*, and *Chaetoceros*) reflect higher food availability for filter-feeders at SH, then differences in benthic community structure (Menge 1992; Menge et al. 1994) may depend partly on variation in

nearshore pelagic community structure. That is, for filter-feeders, higher abundances, higher growth, or both at SH may depend on the higher phytoplankton levels seen there. Alternative explanations exist, however. For instance, different filter-feeder abundance may depend on differences in recruitment (i.e. differences in onshore transport of larvae). Particulate materials, another important food of filter-feeders, were also more abundant at SH and exhibited the same seasonal pattern of variation as did Chl *a* (B. Menge et al. unpubl. data). Two potential physical explanations—that wave forces or flow rates during wave surge differ between sites—can evidently be discounted. Data presented elsewhere (Menge et al. 1995) indicate that neither of these factors differs consistently between BB and SH.

Our results are consistent with the hypothesis that differences in rocky intertidal communities may reflect differences in nearshore pelagic productivity. Although strong links between pelagic events and benthic populations have been suggested elsewhere (e.g. Duggins et al. 1989; Witman et al. 1993), to our knowledge there is only one other comparable example linking rocky shore community-level phenomena to coastal oceanographic events (Bustamante et al. 1995*a,b*). The Bustamante et al. (1995*a,b*) study, done around the South African coast (a scale of 1,000s of km), found that high macrophyte detritus input, with greatest rates in upwelling regions, supported high intertidal grazer biomass. These grazers in turn exerted strong control over in situ macrophyte abundance. Our investigation, which shows consistent between-site differences in productivity at a smaller spatial scale (10s of km), suggests that ecologically significant variation can occur within an upwelling region and that it can be strongly associated with rates of important community processes. This relatively fine-scale effect of phytoplankton input is intriguing and suggests that further study of this phenomenon will provide insights into the nature and strength of links between pelagic ecosystems and benthic communities.

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