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Relative roles of coastal and oceanic processes in determining physical and chemical characteristics of an intensively sampled nearshore system

Catherine A. Pfister and J. Timothy Wootton
Department of Ecology and Evolution, 1101 E 57th St., University of Chicago, Chicago, Illinois 60637

Christopher J. Neufeld
Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada; Bamfield Marine Sciences Centre, Bamfield, British Columbia V0R 1B0, Canada

Abstract

We compared the extent to which offshore and remote-sensing measurements of sea surface temperature (SST), upwelling, and chlorophyll a (Chl *a*) were concordant with in situ measurements of temperature, Chl *a*, and water nutrients at Tatoosh Island, Washington for the past 8 yr. Offshore SSTs were significantly correlated with water temperatures at Tatoosh, though consistently 2°C to 3°C warmer. Sea-viewing wide field-of-view sensor Chl *a* estimates were poor predictors of Chl *a* at Tatoosh Island measured with an anchored fluorometer. Nitrate and phosphorus estimates at Tatoosh Island were positively correlated with an upwelling index and negatively correlated with SST, as would be expected from an upwelling source. In contrast, ammonium and nitrite were uncorrelated with the upwelling index or SST and showed elevated levels immediately adjacent to Tatoosh Island, suggesting strong local effects of marine invertebrates, birds, and mammals on nutrient dynamics and cycling in coastal ecosystems.

Although changes in weather, climate, and ocean circulation can have dramatic effects on species abundance, distribution, and interactions (Sanford 1999; Helmuth et al. 2002; Menge et al. 2003), there is evidence that these large-scale phenomena interact with small-scale and local events. For example, events generated at large scales such as wave energy and the supply of recruits can interact with local consumer–resource interactions to determine abundance and persistence (Robles and Desharnais 2002; Harley 2003). Similarly, wave exposure and nitrogen can interact with consumer abundance to determine the composition and abundance of macroalgae (Nielsen 2001, 2003; Nielsen and Navarrete 2004). Nitrogen can be supplied by large-scale oceanic processes (mainly upwelling) and can also arise from regenerated nitrogen at very local scales (Dugdale and Goering 1967), such as the excretion of nitrogenous wastes by intertidal invertebrates (Bayne and Scullard 1977; Jensen and Muller-Parker 1994; Bracken and Nielsen 2004), perhaps ameliorating periods of nutrient stress. Bird guano and marine mammals are additional sources of regenerated nutrients (Hansen 1981; Bosman et al. 1986; Wootton 1991).

In many cases, correlations between large-scale oceanographic events and local biological responses in intertidal or nearshore populations rely on automated buoy data collection or satellite data (Pfister 1997; Menge et al. 2003; Navarette et al. 2005), while coastal-based sampling has only recently increased (Menge et al. 1997; Hickey and Banas 2003; Grantham et al. 2004). Estimates of ocean productivity are available as Chl *a* estimates from the sea-viewing wide field-of-view sensor (SeaWiFS, NASA) by measuring the reflective spectra at a spatial scale of 1.1 km. The U.S. National Data Buoy Center (NDBC, www.ndbc.noaa.gov) has a network of buoys that remotely and continuously collect information about physical features of the ocean such as sea surface temperature (SST). Upwelling indices are also produced for different latitudes and are based on wind direction and atmospheric pressure. These estimators have the potential to be extremely useful to coastal marine ecologists in predicting local productivity, nutrient availability, the probability of recruitment, etc. However, many of these buoys are tens to hundreds of kilometers from the intertidal and shallow subtidal environments that are intensively studied and important ecologically. Whether these buoys provide accurate information about the water characteristics close to shore is not well understood.

On Tatoosh Island, Washington, SST and chlorophyll *a* (Chl *a*) have been measured since 2000 and water nutrients have been measured since 1998. To test the concordance of large-scale ocean measurements with local measurements, offshore buoys and satellite data were compared with our Tatoosh Island data. Specifically, the goals of our study were to determine whether: (1) absolute and relative patterns in SST were similar at Tatoosh Island

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and offshore buoys; (2) SST and upwelling indices offshore were correlated with our estimates of chlorophyll, nitrate, ammonium, and phosphorus at Tatoosh Island; and (3) Chl *a* measurements from SeaWiFS were concordant with those measured in situ at Tatoosh Island. Finally, we tested if nutrient levels in proximity to Tatoosh Island were elevated in comparison with water at distances from the island.

Methods

Spring and summer water nutrient data were collected beginning in 1998, whereas SST and Chl *a* estimates began in 2000 on Tatoosh Island, Washington State (48°24′N, 124°44′W). Water nutrients, including ammonium, nitrate, nitrite, phosphate, and silica, were measured monthly at 10 sites around Tatoosh Island from April to September. We collected seawater for analysis from shore with a 60-mL syringe during an incoming daytime tide, approximately 2–3 h after mean lower low water (MLLW). The sample was immediately filtered through a GF/C filter into acid-washed high-density polyethylene plastic bottles, placed on ice, and then frozen within 4 h of collection. Water nutrient concentrations (PO_4^{3-}, SiO_4, NO_3^-, NO_2^-, NH_4^+) were analyzed by the Marine Chemistry Laboratory at the University of Washington (methods from UNESCO 1994). The 10 sites on Tatoosh Island include multiple compass orientations and vary in the degree of wave exposure and intensity of currents.

SST, dissolved oxygen (DO), pH, salinity, and Chl *a* concentration (in $\mu g\ L^{-1}$) were measured remotely every 30 min from approximately April to September using a Hydrolab DataSonde 4a (Hach Environmental) with an onboard fluorometer (WETSTAR miniature fluorometer, Wetlabs) and pump (Seabird Electronics). The DataSonde 4a was anchored with stainless steel eyebolts and chain flush against the wall of a large tide pool (4.74 m^2 surface area, 1.09 m depth) at approximately 1.0 m above MLLW. The tide pool was located in a north-facing compass orientation. Every 2 weeks the instrument was removed from the pool and cleaned and the data were downloaded. For the purposes of this study, data were only used at or exceeding a tide height of 1.83 m to ensure that open ocean water was being recorded. Because this criterion was conservative and excluded many readings, we also analyzed data at a cutoff of 1.22 m (the level at which the pool is certain to be flooded) and 1.52 m above MLLW for comparison. When we selected the deployment site, preliminary studies with fluorescein dye showed that the water in the pool was flushed completely within seconds after the tide came in. Furthermore, DO and water temperature measurements made within the pool and simultaneously in adjacent open water with a portable oxygen probe (YSI Model 55) were similar at both low and high tides.

Estimates of offshore SST (°C) were obtained from the Cape Elizabeth buoy (CE, No. 46041) at 47.4°N and 124.5°W, 1.0° to the south and 0.23° to the west of Tatoosh Island (or ~50 km to the southwest). Data are logged once per second during an 8-min averaging period h^{-1} from a sensor at 0.6 m depth; data are available from the NDBC (www.ndbc.noaa.gov). Upwelling indices were obtained for 48°N and 125°W by the National Oceanic and Atmospheric Administration (NOAA) (www.pfeg.noaa.gov) and are reported as an index in $m^3\ s^{-1}$ per 100 m of coastline. The index integrates over a monthly period using surface atmospheric pressure fields to estimate wind-induced coastal upwelling. We also obtained data from a second buoy (Neah Bay [NB], No. 46087) at 48°29′38″N, 124°43′38″W. At 13 km north of Tatoosh Island, the NB buoy is much closer to our study site than No. 46041, but has only been in operation since July 2004.

Chl *a* measurements were obtained from SeaWiFS (courtesy of NOAA) using two regions adjacent to Tatoosh (CPO1 and CPO2). CPO1 is bounded by 125°0′W to 124°42′W longitude and 48°20′N to 48°36′N latitude, while CPO2 is bounded by 124°48′W to 124°42′W longitude, 48°21′N to 48°27′N latitude. Daily and monthly means are reported in mg m^{-3} (equivalent to $\mu g\ L^{-1}$). Because of cloud cover, there were 290 missing values (of 591 daily fluorometer readings) for daily means.

Linear regression was used to model the relation between (1) water temperature measurements from both buoys (both hourly and daily) and Tatoosh Island measurements, and (2) Chl *a* estimated with SeaWiFS (both daily and monthly) and the in situ DataSonde Chl *a* measurements. We examined both the linearity of the relation and the features of the residuals. In all cases the assumption of normality was met on the raw or log-transformed data. Time series was also used to determine whether there was significant lags of 1 to 5 d, which could improve the fit of a regression model.

Autocorrelation and cross-correlation analysis was used on the temperature data from Tatoosh and CE. Autocorrelation analysis was used from each site and year within a 25-d window, and the results were averaged for each site across years. Cross-correlation analysis of data between Tatoosh and CE were also examined, using a window of ±30 d. Average and standard deviation of cross-correlations for each year were determined and tested against the null hypothesis of no consistent deviation from zero using a one-sample *t*-test.

Given that the upwelling index should be a proxy for water nutrient concentrations, we also estimated the correlation between the monthly upwelling index and our monthly estimates of water nutrient concentrations on Tatoosh. We also examined whether rainfall during the previous 24 h (R. T. Paine unpubl. data), which could have transported nutrients and guano off the island and into the water, was responsible for the variation in nitrogen concentration in the water.

We sampled nutrient concentrations by boat at four stations (within a *Nereocystis luetkeana* kelp bed, then ~50 m, 100 m, and 500 m from Tatoosh Island) on an easterly oriented transect. Twenty transects were sampled during May through September from 2000 to 2005. The station inside the kelp bed (20 m from Tatoosh at high tide) was emergent on low tides at 0.0 m MLLW. The collection methods were identical to those described for the sites on Tatoosh. Because there was substantial among-date variance in the estimates of nutrients, we used nonparametric

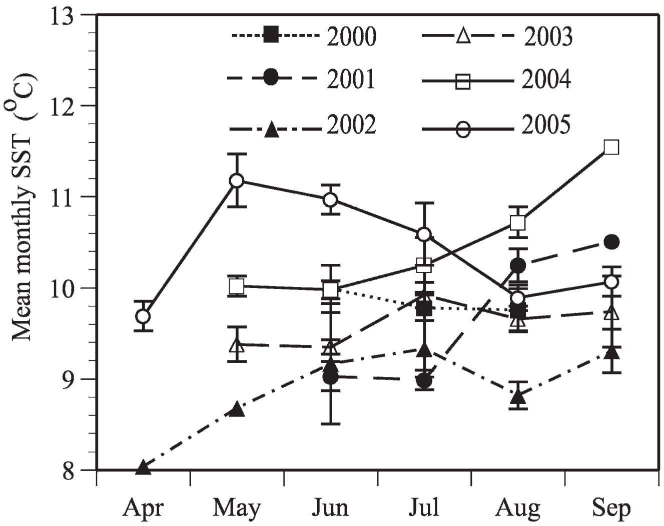

Fig. 1. Mean monthly sea surface temperatures (SST) in °C at Tatoosh Island by year (±SE). Values were estimated from a daily mean using readings every 30 min and selecting only those values where the tide level was +1.82 above MLLW. In some cases, standard errors were smaller than the symbol.

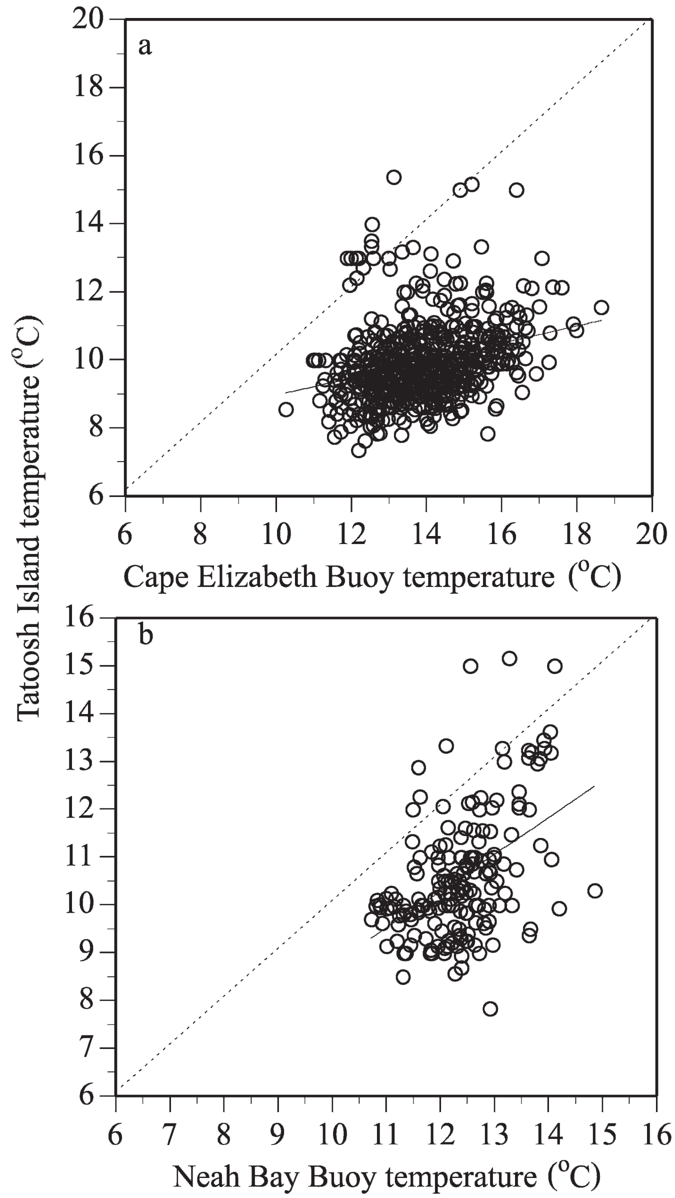

Fig. 2. The mean daily SST (°C) recorded at Tatoosh Island versus (a) Cape Elizabeth buoy over 578 d from 2000 to 2005, and (b) Neah Bay buoy over 177 d from 2004 to 2005. Lines are best fit, with $r^2 = 0.085$, $F_{1,577} = 54.49$, $p < 0.001$ and $r^2 = 0.219$, $F_{1,172} = 49.56$, $p < 0.001$. The dotted line is the 1 : 1 line.

analysis of variance (Kruskal–Wallis) to determine if the sites differed in nutrients. Finally, a simultaneous collection of seawater was used to assess total nitrogen and total phosphorus at one date (02 Sep 05), which allowed us to test whether particulate and organic sources of nitrogen and phosphorus show similar patterns to the inorganic forms. The collection methods were identical except that the water was not filtered.

Results

Temperature—The mean monthly SST at Tatoosh, on the basis of our measurements with the DataSonde 4a, varied significantly among years, with 2002 showing the coolest temperatures, whereas 2004 and 2005 had relatively warmer temperatures (Fig. 1). Water temperatures around Tatoosh Island were on average 2–3°C lower than the CE or NB buoys (Fig. 2a,b). The minimum temperature recorded at Tatoosh was 7.36°C, while the minimum at CE and NB was 10.27°C and 10.73°C, respectively. Maximum temperatures were also greater offshore, with 18.65°C and 14.86°C recorded at CE and NB, respectively, while mean daily temperatures that exceeded 12°C were rare at Tatoosh Island (with the exception of warm water in early July of 2005). Although Tatoosh temperatures were positively correlated with SST at both buoys, there was much scatter about the relation and the r^2 improved little by either using different tide criteria for Tatoosh temperature data (e.g., 1.22 or 1.52 m above MLLW instead of 1.83 m), or by lagging a variable from 1 to 5 d (analyses not provided). Even though the NB buoy has been functional only since July 2004, a regression of the buoy temperature on the DataSonde 4a temperature yielded an r^2 of 21.9% compared with 8.5% for CE, a result that is not explained by sample size. A regression model using month and year showed that later summer months (July, August, September) had the greatest intercepts and thus the greatest disparity compared with Tatoosh. The slope of the relation between temperature at Tatoosh versus CE changed depending upon the month analyzed ($p < 0.001$, test for equality of slopes). Despite these disparities between the offshore CE and inshore Tatoosh site, the temperature range recorded was similar, either within a day (1.15°C range at Tatoosh compared with 0.98°C range at CE) or within a month (3.35°C vs. 3.31°C range, respectively).

The temporal autocorrelations of the two sites, however, exhibited distinctive differences; positive autocorrelations from Tatoosh declined rapidly to zero within a week, whereas those from CE were both initially stronger and

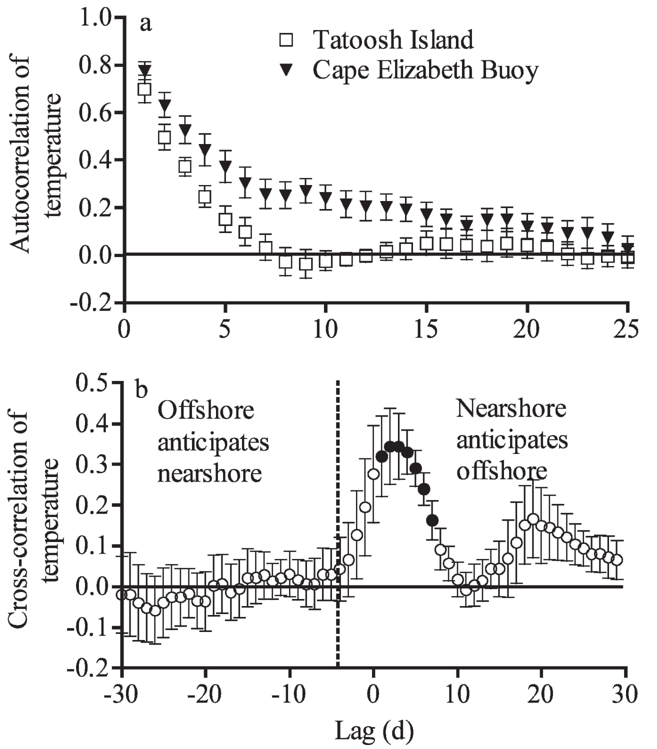

Fig. 3. Time-series analyses of mean daily SST (°C) from Tatoosh and Cape Elizabeth buoy, reported as averages (±1 SE) of values from each sample year. (a) Temporal autocorrelation functions for Tatoosh Island (open squares) and Cape Elizabeth buoy (dark triangles). (b) Cross-correlations of Tatoosh Island and Cape Elizabeth buoy. Negative lags indicate that Cape Elizabeth data precede Tatoosh data, positive lags indicate the opposite. Statistically significant correlations ($p < 0.05$) indicated with filled symbols.

were maintained for 3 weeks or more (Fig. 3a). This difference suggests that Tatoosh temperatures were dominated by shorter-period fluctuations than those at CE, a conclusion supported by spectral analysis (data not shown).

Cross-correlation analysis reinforced the interpretation that offshore conditions provided poor predictive ability for nearshore temperatures. Conditions at CE showed no strong cross-correlations at or before measurements taken at Tatoosh, but measurements taken at Tatoosh exhibit a consistent, though fairly weak ($r < 0.35$), correlation with CE data taken 2–3 d later (Fig. 3b).

Chlorophyll—Chl *a* measurements were characterized by high variability, both via the SeaWiFS data and as measured in situ by our anchored fluorometer. Mean monthly estimates using the Tatoosh fluorometer reveal variation among months and years (Fig. 4), with a mid-season decline similar to that shown for phytoplankton off the California coast (Venrick 1993). SeaWiFS Chl *a* measurements were poor estimators of contemporaneous fluorometer Chl *a* on a daily basis (Fig. 5, $r^2 = 0.001$, $F_{1,289} = 0.392$, $p = 0.532$) on the basis of a linear regression of log-transformed data. The results were unchanged if either 1.22 or 1.52 m above MLLW was used as a criterion

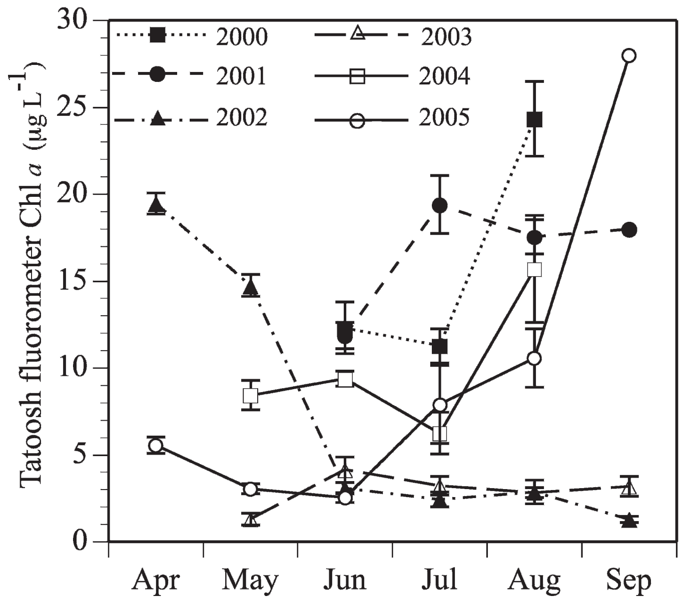

Fig. 4. Mean monthly Chl *a* estimates (μg L^{-1}) at Tatoosh Island by year (±SE). Values were estimated from a daily mean using readings every 30 min and selecting only those values where the tide level was +1.82 above MLLW.

for data selection from the fluorometer data ($r^2 = 0.001$, $F_{1,289} = 0.387$, $p = 0.534$ and $r^2 = 0.001$, $F_{1,289} = 0.392$, $p = 0.532$ respectively). Moreover, when a monthly timescale was used to compare the mean SeaWiFs and fluorometer Chl *a* measurements with the upwelling index, no meaningful relation was found (fluorometer vs. upwelling index, r^2

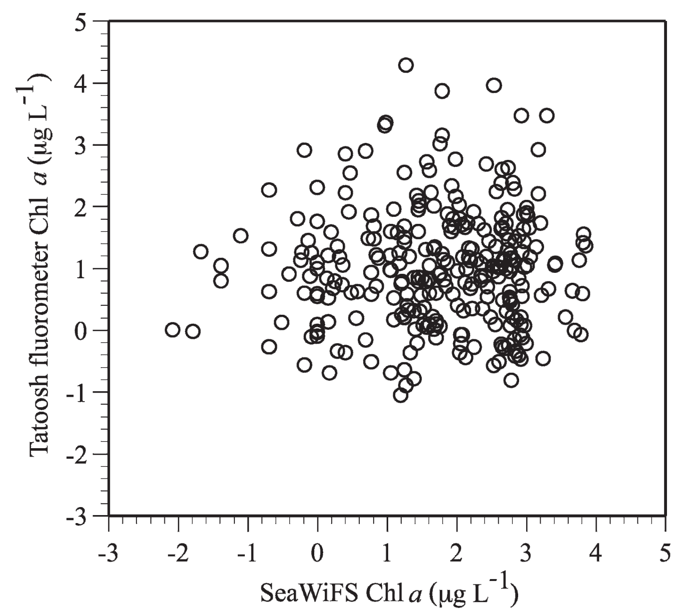

Fig. 5. The relation between Chl *a* estimated in situ at Tatoosh Island versus Chl *a* from SeaWiFS satellite data (μg L^{-1}). Log-transformed daily means are shown. A linear regression using logged data showed that SeaWiFS was a poor predictor of Tatoosh Chl *a* data ($r^2 = 0.001$, $F_{1,289} = 0.392$, $p = 0.532$).

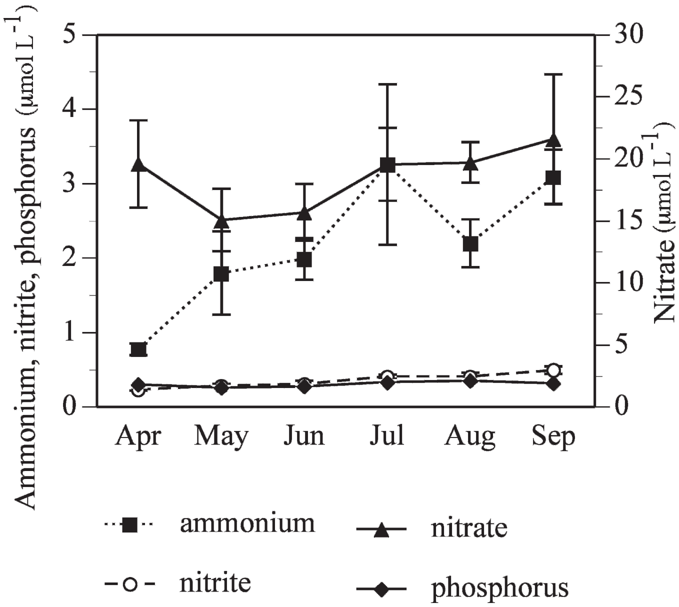

Fig. 6. The yearly mean (±SE) of (a) ammonium, (b) nitrate, (c) nitrite, and (d) phosphorus (in μmol L^{-1}) at 10 sites around Tatoosh Island from 1998 through 2005.

$= 0.100$, $n = 28$, $p = 0.613$; SeaWiFs vs. upwelling, $r^2 = 0.000$, $n = 27$, $p = 0.876$).

Because high variability characterized the Chl *a* measurements using both metrics, we asked whether SeaWiFS was a better predictor of Chl *a* recorded at Tatoosh when only peak Chl *a* measurements were used. However, when we selected data using those days with Chl *a* measurements greater than 10 or 20 μg L^{-1} we still found little evidence for a relation between the two metrics for Chl *a* (Chl *a* > 10 μg L^{-1}: $r^2 = 0.001$, $F_{1,108} = 0.050$, $p = 0.823$; Chl *a* > 20 μg L^{-1}: $r^2 = 0.080$, $F_{1,24} = 2.085$, $p = 0.162$).

We found no evidence that the poor Chl *a* correlations were associated with decreased daytime fluorescence due to reallocation of energy to other cell functions (e.g., MacIntyre et al. 2002); nighttime Chl *a* measurements remained poorly related among sites ($F_{1,271} = 0.698$, $r^2 = 0.003$, $p = 0.404$), and daily estimates for daytime and nighttime DataSonde Chl *a* did not differ (7.74 vs. 8.28 μg L^{-1}, $t = 0.680$, df = 474, $p = 0.496$).

Nutrients—Although mean values for nutrients were relatively high (ammonium = 2.28 μmol L^{-1}, nitrite = 0.37, nitrate = 18.70, phosphate = 1.89), there were periods of relative scarcity of nitrogen, especially in the early spring months (Fig. 6). High spatial variation existed in nutrient levels, as demonstrated by the standard error bars in Fig. 6. Chl *a* recorded at Tatoosh (as a monthly mean) did not show a correlation with water nutrients, whereas the monthly upwelling index did show a positive relation with nitrate and phosphorus, but not ammonium or nitrite (Table 1). Nitrate and phosphorus were positively correlated with each other (0.864, $p < 0.001$), as were ammonium and nitrite (0.479, $p = 0.010$).

Rainfall (in cm) in the previous 24 h explained a significant amount of the variation in ammonium concentrations around Tatoosh (Fig. 7, $F_1 = 4.986$, $r^2 = 0.095$ intercept = 2.045, $p = 0.032$, $n = 39$), suggesting that guano and marine mammal excrement were being washed off the rocks with rainfall. No such relation existed for nitrate ($F_{1,38} = 1.640$, $p = 0.208$).

Table 1. Pairwise correlation coefficients with upwelling index for 48°N monthly, Chl *a*, and SST (recorded on Tatoosh) with water nutrients. $n = 39$ monthly estimates from 2000 to 2005 for the upwelling index and $n = 28$ for SST and Chl *a*; * $0.10 > p > 0.05$, ** $p < 0.05$. The upwelling index and Tatoosh SST were negatively correlated (-0.359, $p = 0.044$), while the upwelling index was uncorrelated with average monthly Chl *a* estimates ($r = 0.100$, $n = 28$, $p = 0.613$).

	Ammonium	Nitrite	Nitrate	Phosphorus
Upwelling index	0.022	0.040	0.276*	0.287*
Mean SST	0.245	0.077	−0.421**	−0.356*
Mean Chl *a*	−0.102	0.261	0.264	0.201

The pattern of nutrient concentration at Tatoosh Island and at three distances from it showed that ammonium, nitrite, and phosphorus were significantly higher inside the kelp bed compared with 50, 100, and 500 m from Tatoosh, whereas there was no such pattern with nitrate (Fig. 8). The pattern for ammonium was especially strong and there were only three instances among all sampling dates that ammonium inside the kelp bed was not greater than the other three locales; in these three instances the difference was only 0.03 to 0.06 μmol L^{-1}. For ammonium, nitrite, and phosphorus, the samples taken inside the kelp bed were very similar to those taken from the shore at Tatoosh.

Organic nitrogen (total nitrogen minus inorganic forms) showed a pattern similar to that of ammonium and nitrite, with higher values at the 10 sites around Tatoosh (mean = 8.65 μmol L^{-1} ± 0.98 SE) and inside the kelp bed

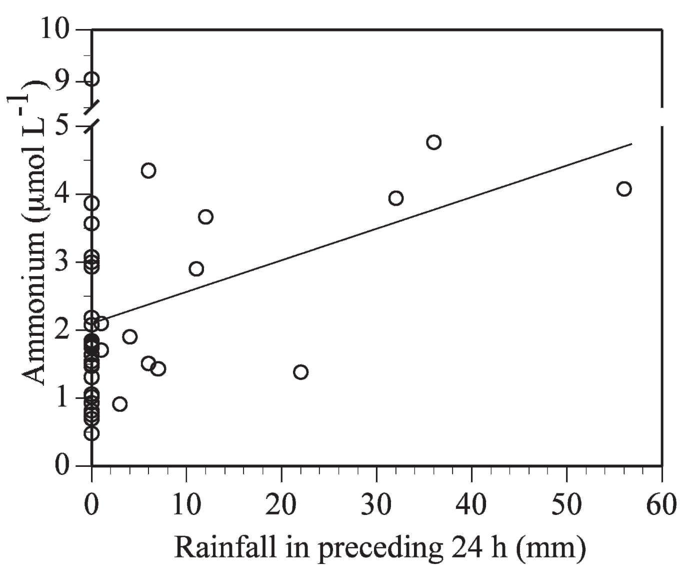

Fig. 7. The relation between the mean ammonium at 10 Tatoosh sites and rainfall in the previous 24 h. Rainfall explained a significant amount of variance in ammonium levels ($r^2 = 0.095$, $F_{1,38} = 4.986$, $p = 0.032$).

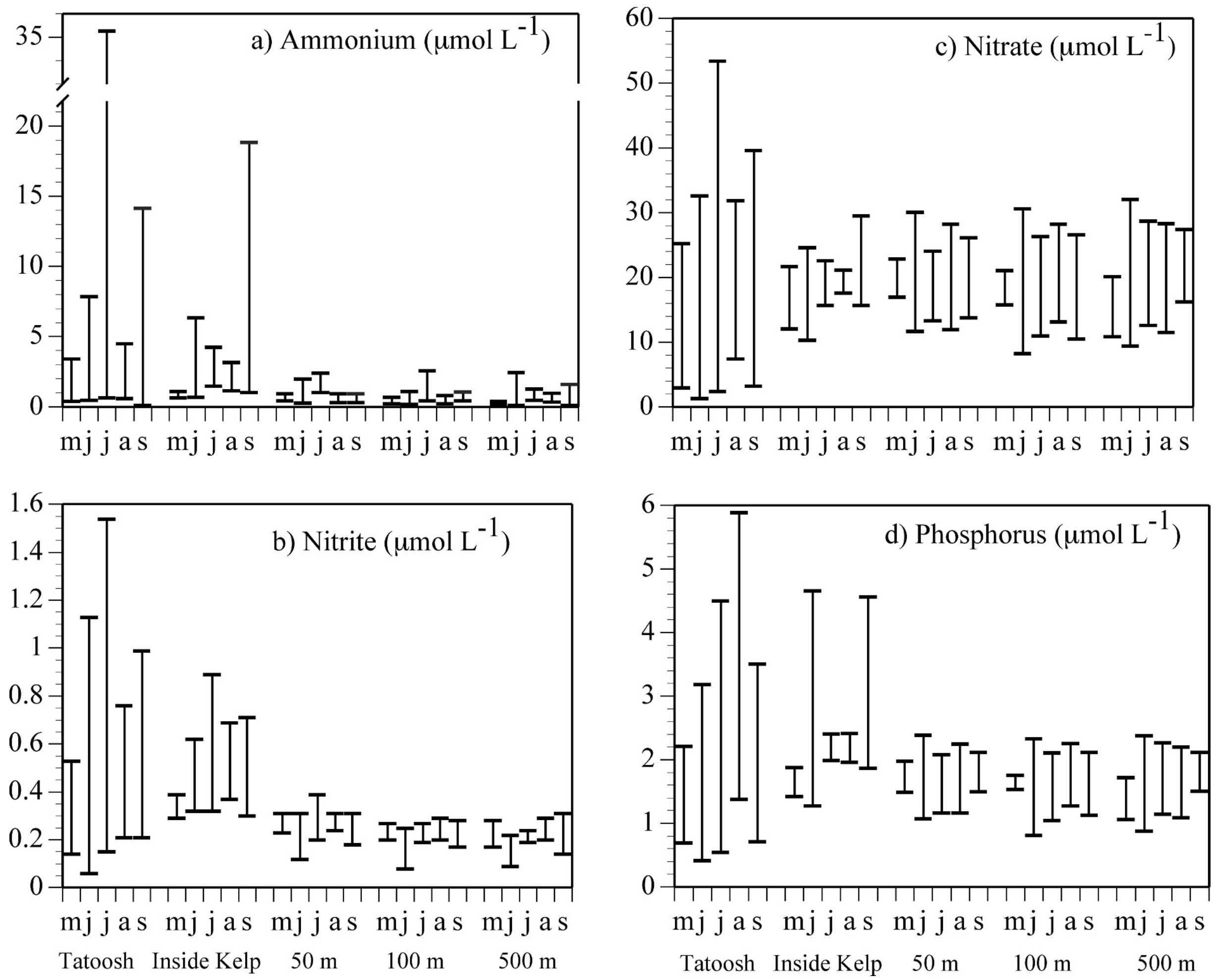

Fig. 8. The range of estimates for (a) ammonium, (b) nitrite, (c) nitrate, and (d) phosphorus (μmol L^{-1}) at 10 sites on Tatoosh Island with a corresponding single sample from inside the kelp bed, and 50, 100, and 500 m from the Island. Minimum and maximum values are shown for 20 spring and summer sampling dates from 2000 to 2005. A comparison of the 'inside kelp' sample with the three further samples at each date showed that ammonium, nitrite, and phosphorus were significantly greater inside the kelp than away from Tatoosh (Kruskal–Wallis = 24.6 [$p < 0.0001$], 44.98 [$p < 0.0001$], 9.22 [$p = 0.027$], respectively). Nitrate showed no pattern (Kruskal–Wallis =1.09, $p = 0.780$).

(10.53 μmol L^{-1}), compared with 50 (4.73 μmol L^{-1}), 100, (1.53 μmol L^{-1}), and 500 m (3.83 μmol L^{-1}) from the island. Organic phosphorus (total phosphorus minus phosphate) also showed a decline away from the island, with a Tatoosh mean of 0.39 μmol L^{-1} ($\pm$0.06 SE) and 0.45 μmol L^{-1} inside the kelp bed, declining to 0.19, 0.16, and 0.17 μmol L^{-1} with distance from the island.

Discussion

Concordance of satellite and buoy data with Tatoosh Island monitoring—SSTs from ocean buoys, though correlated with Tatoosh seawater temperatures, were relatively poor predictors of Tatoosh seawater temperatures. Estimates of r^2 were typically low when buoy temperature was regressed on Tatoosh temperatures and the relation was characterized by high variation around the best-fit line. Additionally, offshore water conditions did not anticipate nearshore water patterns at later times. Instead, nearshore conditions provided predictive information about offshore conditions 2–3 d later, although the strength of these predictions was weak ($r = 0.343$). This situation may arise if strong currents that flow out of nearshore areas such as the Strait of Juan de Fuca develop occasionally from mechanisms such as variations in tidal flow and strong offshore winds, and subsequently perturb the predominating offshore currents and eddies. Interestingly, temperatures nearshore tended to be 2°C to 3°C colder, perhaps reflecting the localized upwelling of deeper, colder water that is thought to be associated with the Juan de Fuca Eddy (Hickey and Banas 2003) or interactions with bathymetric features. The autocorrelation results indicate that Tatoosh temperatures vary more rapidly than those observed offshore, which could explain the relatively poor ability of offshore data to predict nearshore conditions.

Chlorophyll estimated from SeaWiFS satellites were poor predictors of Chl *a* from the Tatoosh fluorometer. Chl *a* estimates were typically characterized by high variability with periods of low Chl *a* concentrations punctuated by high values. However, the satellite data were not consistent with our Tatoosh fluorometer even when we looked only at the peaks in Chl *a* concentration. Even though the daytime fluorometer estimates could have underestimated Chl *a* because of reallocation to other cell functions and reduced daytime fluorescence (e.g., MacIntyre et al. 2002), the relation between nighttime SeaWiFS and fluorometer readings was not improved.

There are several reasons, both methodological and biological, that might lead to poor agreement between these two metrics of Chl *a*. First, terrestrial environs can interfere with satellite estimates of Chl *a* (Hu et al. 2000). Second, submerged fluorometers need regular cleaning and can be difficult to calibrate with natural phytoplankton assemblages. A third explanation is that the phytoplankton assemblage near Tatoosh is different from that offshore, a possibility based on differences in physical parameters (Hickey and Banas 2003; MacFadyen et al. 2005; Tinis et al. 2006). This feature, in tandem with turbulent tidal mixing, may serve to make the waters surrounding Tatoosh Island colder and nutrient rich with different phytoplankton. However, what Chl *a* reveals about the ocean environment in this region is unclear from our data. Chl *a* estimated by either methodology was unrelated to any nutrient estimated or to the upwelling index or seawater temperature. Thus, a possibility is that the phytoplankton do not respond linearly to physical aspects of the estimated water conditions at the site and their abundance is related to factors at different timescales or only at threshold values (Huppert et al. 2002). However, there is no evidence of this in our data and rank statistics did not improve the correlation among variables. Alternatively, the relative abundance of nitrogen may lead to variance in phytoplankton abundance that is unrelated to upwelling or the water column nutrients that we estimated, and is perhaps more a function of turbulent mixing (Smetacek and Passow 1990), other micronutrients such as iron (Coale et al. 1996; Hutchins et al. 1998), or zooplankton grazing (Landry et al. 2000). A lack of correspondence between Chl *a* and nitrate and phosphorus was also reported by Menge et al. (1997) for coastal Oregon and we note that our Chl *a* estimates were in a range similar to theirs.

Diverse sources for the supply of nitrogen?—Nutrients were relatively high in concentration surrounding Tatoosh Island, often exceeding estimates for other locales in the northeast Pacific Ocean, such as sites along the Oregon coast (Menge et al. 1997; Corwith and Wheeler 2002). There were, however, periods of low nutrient concentration, particularly in the early spring. Although not measured here, winter months may also be a period of low nutrients (Menge et al. 1997). A conspicuous pattern of rising ammonium and nitrite was seen annually from spring through the summer months, and annual nitrate and phosphorus pulses were correlated with maximal upwelling. Thus, despite the possibility that the Juan de Fuca Eddy has strong local effects on nutrients and productivity, large-scale oceanic upwelling does appear to leave a signature in our nitrate and phosphorus measurements.

A further suggestion that some large-scale oceanic events are detectable at Tatoosh Island comes from the 2005 temperature anomaly. The spring and early summer of 2005 were characterized by relatively high seawater temperatures and low Chl *a* and nitrate in nearshore waters (Figs. 1, 4, 6, Hickey et al. 2006). These water characteristics were also obvious in our data, and the onset of colder, more nutrient-rich water in July 2005, suggested to be forced by upwelling favorable winds in Northern California (Hickey et al. 2006), coincides with what was recorded by our DataSonde and nutrient collection at Tatoosh Island.

The correlation between upwelling and nitrate and phosphorus is expected (Dugdale and Goering 1967); the lack of correlation of upwelling with ammonium and nitrite suggests that these two nutrients have a different source. The supply of nutrients to marine ecosystems has been differentiated into new versus regenerated forms, where new forms include nitrate that has accumulated in deep waters below the photic zone and has been recently upwelled (Dugdale and Goering 1967). The high concentrations of ammonium we estimated at Tatoosh suggest that it is 'regenerated' and being supplied locally. Because autotrophs may have different affinities for each form of nitrogen (Bracken and Stachowicz 2006), it is of interest to know the relative abundance and source of each.

There are many potential sources of ammonium at Tatoosh, including atmospheric deposition, terrestrial plant sources, and the excrement of a variety of species. The positive correlation between rainfall and ammonium suggests that guano and marine mammal excrement that accumulates between periods of rainfall may contribute to this correlation. Tatoosh Island is visited by numerous marine mammal species and is also a locale for breeding birds. At Año Nuevo on the northern California coast, which is a breeding area for marine mammals, water column ammonium peaks are coincident with pinniped biomass (Hansen 1981). The positive intercept in the relation between rainfall and ammonium and the relatively high ammonium at zero rainfall further suggests a role for excretion by marine invertebrates. Finally, marine invertebrates such as mussels and anemones have also been shown to be a source of ammonium (Bayne and Scullard 1977; Jensen and Muller-Parker 1994; Bracken 2004) and are a dominant species on Tatoosh shores (Paine 1974, 1984; Wootton 1993). Invertebrate excretion as a source of ammonium is also supported by experimental manipulations of mussels in tide pools (Pfister 2007) and the striking pattern of ammonium and nitrite decline with distance from the island (Fig. 8).

The relatively high levels of ammonium during the summer have two implications. First, ammonium may ameliorate periods of low nitrogen and reduced upwelling noted during El Niño Southern Oscillation (ENSO) events. Second, the strong concordance between ammonium and nitrite around Tatoosh Island suggests microbial nitrification of ammonium to nitrite (Capone 2000; Ward 2000). Both possibilities suggest that important components of the coastal nitrogen cycle may currently be underestimated.

Large-scale oceanic data and local ecological studies—The relatively poor concordance between large-scale oceanic data (SST, SeaWiFS Chl *a*, upwelling index) and data collected in situ on Tatoosh Island indicate the need for better coastal-based estimates of ocean condition. In all of our analyses, r^2 values were very low, indicating that offshore SST data, Chl *a* from SeaWiFS, and upwelling indices are relatively poor predictors of Tatoosh nutrient, Chl *a*, or SST. For example, although SST could be correlated between offshore buoys and Tatoosh Island, the differences between daily mean SST was often dramatic. The consistency in these differences (Tatoosh Island was always colder) suggests that offshore buoys are simply not capturing the coastal oceanography of the area. Additionally, the nutrient data for Tatoosh Island indicate that the dynamics of inorganic nitrogen are biologically mediated and perhaps not closely tied to the ocean metrics that are currently used to make predictions about oceanic productivity and the intensity of ENSO events. Because of the dependence of remote-sensing data for ecological inference (Schoch et al. 2006), the importance of nearshore areas to productivity, fisheries, and human use (Cohen et al. 1997; Jackson et al. 2001), and the drastic changes shown in the nitrogen cycle (Vitousek 1997; Howarth et al. 2000), an increased understanding of nearshore water conditions is warranted.

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