

Nutrient loading and consumers: Agents of change in open-coast macrophyte assemblages

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Human activities are significantly altering nutrient regimes and the abundance of consumers in coastal ecosystems. A field experiment in an open-coast, upwelling ecosystem showed that small increases in nutrients increased the biomass and evenness of tide pool macrophytes where consumer abundance and nutrient loading rates were low. Consumers, when abundant, had negative effects on the diversity and biomass of macrophytes. Nutrient loading increases and consumers are less abundant and efficient as wave exposure increases along open coastlines. Experimentally reversing the natural state of nutrient supply and consumer pressure at a wave-protected site to match wave-exposed sites caused the structure of the macrophyte assemblage to converge on that found naturally in wave-exposed pools. The increases in evenness and abundance were driven by increases in structurally complex functional groups. In contrast, increased nutrient loading in semi-enclosed marine or estuarine ecosystems is typically associated with declines in macrophyte diversity because of increases in structurally simple and opportunistic functional groups. If nutrient concentration of upwelled waters changes with climatic warming or increasing frequency of El Niños, as predicted by some climate models, these results suggest that macrophyte abundance and evenness along wave-swept open-coasts will also change. Macrophytes represent a significant fraction of continental shelf production and provide important habitat for many marine species. The combined effects of shifting nutrient regimes and overexploitation of consumers may have unexpected consequences for the structure and functioning of open-coast communities.

Human impacts on biogeochemical cycles (e.g., rates of carbon emissions and nitrogen fixation) and on population size of consumers (e.g., by overfishing) can have strong effects on the biodiversity and functioning of ecosystems (1, 2). The effects of consumers on benthic marine ecosystems are renowned as textbook classics in ecology (3–6); however, the role of nutrient supply and its interaction with the effects of consumers are relatively unexplored in these systems (ref. 7, but see ref. 8).

Nitrogen is generally considered to be the limiting macronutrient in most marine ecosystems. Anthropogenic nitrogen inputs to coastal zones from terrestrial sources have already resulted in the eutrophication and degradation of many semi-enclosed coastal ecosystems (e.g., estuaries, bays, and inland seas) worldwide (9). Transport of fixed inorganic nitrogen from the land to the coastal zone has increased 2- to 20-fold in the North Atlantic since preindustrial times (10); global rates are predicted to double by 2050 (11). Those coastal marine ecosystems characterized by limiting natural nutrient levels, high water residence times, and large inputs from terrestrial sources may be particularly vulnerable to increased nutrient loading from rivers and other terrestrial sources (e.g., the Gulf of Mexico and the Baltic Sea; refs. 12 and 13). In contrast, open, wave-swept coastlines along the eastern margins of ocean basins may be more impervious to anthropogenic nutrient inputs because nitrogen is thought to be less limiting because of the large amount of new nitrogen supplied by coastal upwelling (14, 15).

Coastal upwelling, driven by equatorward winds and the Coriolis effect, is the primary mechanism resulting in the

transport of deep, nutrient-rich waters into open-coast ecosystems. Approximately half the global nitrate flux onto continental shelves from the deep sea occurs in coastal upwelling ecosystems (15). Anthropogenic increases in nutrient loading are generally known to be associated with shifts in the abundance and functional diversity of primary producers in bays, estuaries, river-dominated inner-shelves, and inland seas (12, 13). However, in open-coast ecosystems only recently have researchers begun to document a strong association between ecological functioning and variation in upwelling dynamics (16–20).

Unfortunately, most climate change models do not address coastal upwelling, but those that do predict that shifts in ocean–atmosphere circulation patterns are likely to alter upwelling dynamics and thus change inputs of nutrients to coastal ecosystems (21–23). However, the direction of that change with respect to nutrient supply is uncertain. For example, under one global warming scenario, Bakun (23) and Peterson *et al.* (21) predict increased alongshore wind stress and intensification of upwelling, suggesting increased nutrient supply, but Peterson *et al.* (21) predict the nutricline will be depressed, thereby reducing the inorganic nutrient concentration of water entrained by wind-driven upwelling.

Here I describe results from a field experiment, in an open-coast upwelling ecosystem, that demonstrates a strong effect of variation in nutrient supply on the abundance and evenness of benthic macrophytes, where consumer abundances were low. Although it is common knowledge that fertilizer will help a garden grow or a lake to bloom, many littoral fringe ecologists have not considered nutrient limitation possible in open-coast benthic macrophyte assemblages, especially in upwelling ecosystems (24). The dramatic changes in the structure of an intertidal macrophyte assemblage as a result of relatively small changes in nutrient supply documented here suggest that open-coast marine communities are more sensitive to fluctuations in nutrient regimes than previously appreciated. These results also suggest nutrient effects are likely to be amplified where consumers are overexploited or naturally low in abundance. Additionally, because macrophytes account for a significant fraction of annual primary production on continental shelves (25–31), changes in their abundance, productivity, or functional diversity may have important consequences for ecosystem functioning.

Materials and Methods

I manipulated the supply of nutrients and the abundance of herbivores in 42 identical tide pools chiseled into intertidal rock benches on the central coast of Oregon and quantified the abundance of all macrophytes for 2 years (32). The response of the macrophyte community was evaluated through changes in total abundance (percentage cover and biomass) and the abundances of species and functional groups. Functional groupings can improve the resolution of ecological signals by capturing a larger fraction of the functional variance organisms display in relationship to physiological and environmental constraints,

Abbreviation: DW, dry weight.

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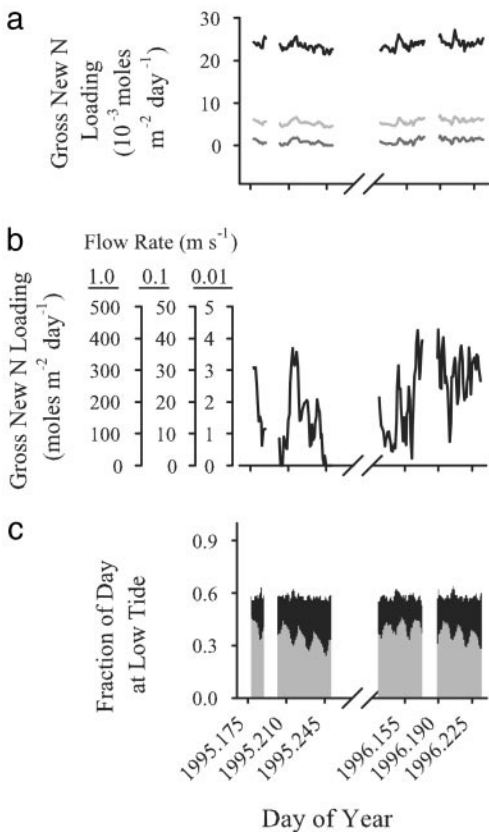


Fig. 1. Gross new nitrogen (N) loading to tide pools. (a) N loading during low tide. (b) N loading during high tide. (c) Fraction of day that the pools were isolated from the ocean during day- and nighttime low tides. Loading rates were estimated by using a single-compartment model assuming unidirectional flow through the volume of the tide pool (65). Ambient new N (nitrate) concentrations were estimated from *in situ* temperature records, average release rates of new N (nitrate and ammonium) from dispensers for each treatment (32), and daily water residence times calculated from tidal height predictions. The relationship between temperature (°C) and nitrate concentration (μM) from shore-based samples taken in Oregon between 1993 and 1999 used in the model was $[\text{NO}_3] = T^{-1}(487.4) - 32.4$; $r^2 = 0.61$, $n = 246$, $P < 0.0001$. Loading rates were calculated for four periods when dispensers were deployed and data were available (temperature data were lost during the beginning of the first deployment). Loading to tide pools during high tide was calculated for a range of possible flow rates through the pools (see Fig. 2 for context); absolute flow rate was not measured (see Results for details). Black line, ambient N loading; light gray line, low N addition; dark gray line, high N addition; gray shading, daytime; black shading, nighttime.

especially in species-rich systems (33–35). Furthermore, in marine ecosystems, episodic nutrient supply (because of intermittent upwelling events, or during tidal emersion), in combination with variation in macrophyte nutrient uptake rates, storage capacities, and growth rates, is hypothesized to play an important role in determining the ecological performance of functional groups (36, 37).

I increased nutrient supply with controlled-release nutrient dispensers while the pools were isolated during low tide over two \approx 6-week periods during spring and summer of each year (Fig. 1). I compared three levels of nutrient supply: ambient (no nutrients added), and low and high addition treatments (Fig. 1a). Ambient nutrient concentrations fluctuate naturally through time; during spring and summer they vary in concert with the frequency and duration of upwelling events (Fig. 1a and b). Nutrient supply to benthic organisms is also influenced by flow rates, water residence times, the texture of the uptake surfaces (e.g., the mac-

rophyte canopy), and topographic relief of the rock surfaces (refs. 38 and 39; Figs. 1a and 2). During low tides, nutrient additions consistently elevated average nutrient supply relative to ambient conditions (Fig. 1a; ref. 32). During high tide, nutrient supply did not differ among treatments because the dispenser release rates were low relative to ambient loading rates [high flow rates and low residence times of water in the pools during high tide dramatically increase ambient loading (32); compare Fig. 1a and b]. In Oregon, extreme low tides in the spring and summer occur primarily during daylight hours (Fig. 1c); therefore, increasing nutrient supply during low tide alone could relieve nutrient limitation during a critical growth period.

I simultaneously manipulated the abundance of herbivores in the pools, because they are known to have strong effects on macrophyte diversity and abundance (6, 35). The dominant herbivores in this system were the black turban snail, *Tegula funebralis*, several limpets, *Lottia* spp., periwinkles, *Littorina scutulata*, and hermit crabs, *Pagurus hirsutiusculus*. The abundance of herbivores and their interactions with macrophytes vary across intertidal landscapes, changing dramatically over environmental gradients (40). For example, local productivity can exceed consumption rates, and even reverse the sign and nature of a plant–herbivore interaction, leaving herbivores overwhelmed by macrophytes and competing with them for space (40, 41). Macrophytes must also pass through small life history stages that are vulnerable to consumers. Spatial or temporal refugia from herbivores can result in an opportunity for plants to grow beyond a vulnerable size (42). Differences in resource supply can change the rate of growth to a less vulnerable size, reducing the window of vulnerability and increasing macrophyte abundance even in the presence of herbivores. Because herbivore effects on both macrophyte abundance and diversity may vary with nutrient supply, it was important to characterize nutrient effects over a range of herbivore abundances.

I established two herbivore abundance treatments to span the range of naturally occurring abundances at this site. Herbivore abundances were manipulated by using a combination of barrier methods (32). The tide pools were located in a wave-protected area where average herbivore abundance was naturally high [range = 309.4–525.0 g of dry weight (DW) per m² in pools without barriers]. The barriers reduced herbivore biomass by an order of magnitude (range = 37.5–55.6 g of DW per m²), close to the levels observed in more wave-exposed areas where natural average abundances were much lower (range = 78.1–113.8 g of DW per m²).

Results

Nutrients significantly increased total macrophyte biomass, especially where herbivore abundance was low, primarily through an increase in the abundance of two functional groups (Fig. 3a, Tables 1 and 2). Gross primary productivity was also quantified on a randomly selected subset of the tide pools (32) and was positively correlated with macrophyte biomass (summer 1995, $P < 0.0014$, $r^2 = 0.69$, $n = 21$; summer 1996, $P < 0.0019$, $r^2 = 0.59$, $n = 34$). A diverse suite of 17 red algal species in 17 genera, comprising two functional groups of macrophytes, was more abundant in the high nutrient addition treatment than under ambient conditions (Fig. 3a, Table 1). The increase in abundance of these functional groups had a marginal effect on functional evenness (Table 2) and was greatest where herbivore biomass was low (Tables 1 and 2). Herbivores had a strong negative effect on macrophyte abundance and diversity (Fig. 3a, Table 2). Although nutrients increased total macrophyte abundance and functional evenness only where herbivore biomass was low (Table 2 and Fig. 3a), they significantly influenced the abundances of functional groups across all levels of herbivory (Table 1). Therefore, nutrient effects on the structure of macrophyte

Table 1. Multivariate analysis of covariance of the effects of nutrients and herbivore biomass (covariate) on the abundance of macrophyte functional groups

Effect	df	Wilks' Lambda	F	P value
Nutrients (N)	14, 50	0.4003	2.07	0.0303
Herbivore biomass (H)	7, 25	0.1501	20.22	<0.0001
N × H	14, 50	0.5432	1.27	0.2563
Blocks*	35, 107.6	0.0612	2.90	
Nutrient treatment contrasts				
N: ambient vs. low addition	7, 25	0.7700	1.07	0.4128
N: low addition vs. high addition	7, 25	0.6304	2.09	0.0822
N: ambient vs. high addition	7, 25	0.5071	3.47	0.0098

The response variables are the average abundances of functional groups: filaments, polysiphonous/thinly corticated, thin blades, heavily corticated, articulated corallines, fleshy crusts, and coralline crusts (35). Filaments, polysiphonous/thinly corticated, thin blades, and heavily corticated functional groups were square-root transformed to meet the assumption of homogeneity of variances. Diatoms were not included because they were too scarce to meet assumptions of the statistical analysis. Examination of the individual analysis of covariance for each functional group suggests that nutrient effects are important for polysiphonous/thinly corticated ($P = 0.0102$, $F_{2,31} = 5.33$) and heavily corticated ($P = 0.0236$, $F_{2,31} = 4.24$) algae, whereas herbivore effects are important for all functional groups (all $P < 0.0085$) except articulated corallines ($P = 0.6172$, $F_{1,31} = 0.25$), and fleshy crusts where there is an interaction with nutrients ($P = 0.0497$, $F_{2,31} = 3.31$).

*Blocks were modeled as a random factor.

assemblages are likely to be most apparent where herbivore abundances are low or in naturally occurring refugia.

As expected from previous studies (6, 35), high herbivore biomass reduced total abundance, as well as functional richness, diversity and evenness of macrophytes (Fig. 3, Tables 1 and 2). Average macrophyte species richness was also negatively affected by increasing herbivore biomass (g DW) (no. of species = $7.95 - 0.027 \times$ herbivore biomass (H), $P < 0.0001$, $r^2 = 0.52$, $n = 42$); there was no evidence of a nutrient effect on species richness (analysis of covariance: nutrients (N), $P = 0.68$, $F_{2,31} = 0.40$; H, $P < 0.0001$, $F_{1,31} = 29.64$, N × H, $P = 0.34$, $F_{2,31} = 1.11$).

The effects of herbivores and nutrients on the structure of macrophyte assemblages changed over time. The effect of herbivores on macrophyte species richness changed significantly over time (repeated measures multivariate analysis of covariance, H × time, $P < 0.0001$, $F_{5,63} = 7.87$); both the magnitude and the percentage of variance explained by herbivory declined over time (Table 3). However, the impact of herbivores on macrophyte functional group abundances was strong throughout the two years of the experiment (Table 4). In contrast, nutrient effects became evident only during the second year (Table 4). These results suggest that species with similar traits (within a functional group) were able to persist and flourish, but competition among species within a functional group for other resources (such as space or light) may have limited species richness (43).

Increasing the abundance of structurally complex functional groups may increase the capacity of the community for nutrient storage, a property that would likely increase the community's persistence during short-term low nutrient periods (36, 37, 44). Increased nutrient supply in this experiment did enhance the ability of more structurally complex species (with less opportunistic life history strategies and slower growth rates) such as the corticated algae to attain high abundances, but not until the second year (Fig. 3a, Tables 1 and 4). Once established, more structurally complex forms may also generate time lags or buffer community responses to change in average conditions. Thus the effects of changes in nutrient supply may not be immediately evident.

I found complementary evidence of the relationship between nutrient dynamics and community structure by comparing results of field experiments from nutrient-limited and -nonlimited portions of an environmental gradient. I conducted a similar experiment concurrently at an adjacent location where water motion was greater (more wave-exposed) and herbivores were naturally less abundant. Nutrients were not limiting here, probably because of greater mass transport rates (e.g., Fig. 2). Relative mass transport rates (measured by dissolution of chalk blocks; ref. 45) were 60% greater at the more wave-exposed site (ANOVA: $P < 0.0001$, $F_{1,14} = 102.32$). At this more wave-exposed location there was no evidence for effects of nutrient additions on macrophyte biomass, abundances of functional

Table 2. Analysis of covariance of the effects of nutrients and herbivore biomass (covariate) on average macrophyte biomass, functional richness, diversity, and evenness over all monitoring periods

	df	Biomass* ($r^2 = 0.68$)		Richness† ($r^2 = 0.57$)		Diversity‡ ($r^2 = 0.58$)		Evenness§ ($r^2 = 0.47$)	
		F	P	F	P	F	P	F	P
Full model	10, 31	6.52	<0.0001	4.68	0.0004	4.41	0.0007	2.79	0.0139
Nutrients (N)	2, 31	6.16	0.0056	1.68	0.2023	1.99	0.1540	1.76	0.1884
Herbivores (H)	1, 31	7.56	0.0099	18.35	0.0002	34.21	<0.0001	19.24	0.0001
N × H	2, 31	6.76	0.0037	2.83	0.0745	3.19	0.0560	3.38	0.0471
Blocks¶	5, 31	7.36		2.04		0.42		0.80	

*Macrophyte biomass (g ash-free DW) was estimated from percentage cover (32).

†Functional richness (F) is the number of functional groups. See Table 1 legend for description of functional groups.

‡Functional diversity, Shannon index of diversity, $H' = -\sum p_i \ln p_i$, where p_i is the proportional abundance of functional group i .

§Functional evenness, $H'/\ln F$.

¶Blocks were modeled as a random factor.

Table 3. Regression analysis of the effect of herbivores on species richness for each monitoring period

Season	r^2	P value	Slope	Intercept
Spring 1995	0.12	0.0227	-0.01	4.42
Summer 1995	0.72	<0.0001	-0.06	10.47
Fall 1995	0.25	0.0008	-0.03	8.12
Spring 1996	0.33	<0.0001	-0.03	8.78
Summer 1996	0.17	0.0066	-0.02	9.18
Fall 1996	0.00	0.8281	0.00	6.72

groups, or diversity (analysis of covariance, $P > 0.40$ for all N and $N \times H$ effects). However, experimentally changing the environmental conditions in wave-protected pools to more closely match the natural conditions in wave-exposed pools (by increasing mass transport of nutrients and reducing herbivore abundance) caused the structure of wave-protected pools to converge on that of wave-exposed pools. Total macrophyte biomass, functional group abundances, and functional diversity and evenness in wave-protected pools with high nutrient additions and low levels of herbivory were indistinguishable from wave-exposed pools under natural conditions [ANOVA or multivariate analysis of variance, all P values >0.27 ; compare Fig. 3 *a* and *b*]. There was a significant increase in functional richness with wave exposure, associated with the appearance of kelps in the more wave-exposed pools (ANOVA, $P = 0.04$, $F_{1,10} = 5.53$; the difference in the least-squares estimates of mean functional richness was 1; Fig. 1 *a* and *b*). The striking convergence of community structure in these two treatments strongly suggests that variation in nutrient mass transfer rates contributes to variation in the structure of intertidal macrophyte assemblages across wave exposure gradients. Additional factors that contribute to variation in the structure of macrophyte assemblages over wave exposure gradients include: (i) reduced herbivore biomass and efficiency (46, 47) and (ii) increased light utilization efficiency of kelps with increasing wave exposure (24, 48).

Discussion

Changes in the diversity and abundance of primary producers can strongly influence ecosystem processes in terrestrial systems and may have similar consequences in open-coast ecosystems (49). Global changes in biogeochemical and atmospheric cycles, over-fishing, and coastal development are likely to continue to affect coastal ecosystems. Much of our understanding of how nutrients affect marine communities has been based on the obvious effects of direct, anthropogenic nutrient loading in semienclosed coastal marine ecosystems. The results presented here differ from what we have learned from semienclosed marine ecosystems, where nutrient loading and diversity are often naturally low.

In semienclosed marine ecosystems, increased nutrient loading increases the abundance, but decreases the diversity of

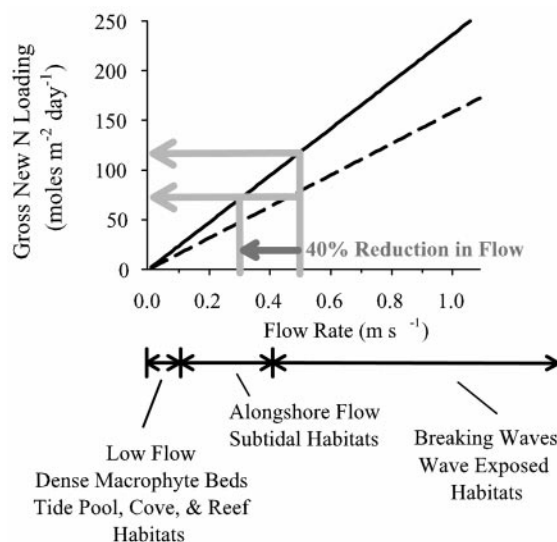


Fig. 2. Variation in gross new N (nitrate) loading associated with flow, N concentration, and habitat type in marine ecosystems. Loading was modeled as a function of average water temperature (see Fig. 1) and flow rate. The domain of flow rates observed in different marine habitats (66, 67) is indicated below the x axis. The gray arrows illustrate the change in loading associated with a 40% reduction in flow rates (similar to that observed across an intertidal wave exposure gradient; see Discussion) under average summer conditions (solid line) and during conditions representative of an El Niño year when water temperatures are elevated and N loading is reduced (dashed line).

marine macrophytes (8, 13). Consumers are often ineffective in controlling the fast-growing and competitively superior annual, ephemeral or epiphytic macro- and microalgae that become abundant (50). Typical results include the following: reduced depth distribution of macrophytes as phytoplankton blooms reduce light levels (51, 52), overgrowth and shading of perennial algae by epiphytes, or shading of eelgrasses by blooms of macroalgae (53). Consumers can increase diversity (8) by consuming these competitively superior and anatomically simple functional groups (6). Surprisingly, and in sharp contrast to results in bays and estuaries, increased nutrient loading in the Oregon open-coast resulted in increased total macrophyte abundance, but not with opportunistic, ephemeral, or anatomically simple functional groups. Instead, less opportunistic and more anatomically complex functional groups responded, increasing evenness and tending to increase diversity. Herbivore effectiveness was not reduced with nutrient loading; rather, wave-exposure appeared to be more important in limiting their effectiveness and abundance (32).

This experimental test of the interactive effects of nutrients and consumers, over naturally occurring gradients of nutrient loading and consumer abundances, provides a new window through which

Table 4. Summary of seasonal changes in treatment effects on the abundance of macrophyte functional groups

Season	Herbivore biomass (H)		Nutrients (N)		H × N	
	$F_{7,25}$	P	$F_{14,50}$	P	$F_{14,50}$	P
Spring 1995	7.92	<0.0001	1.46	0.1712	0.97	0.4915
Summer 1995	7.52	<0.0001	1.70	0.0848	1.66	0.0960
Fall 1995	5.56	0.0006	1.34	0.2167	0.88	0.5880
Spring 1996	10.09	<0.0001	3.27	0.0010	1.95	0.0425
Summer 1996	10.09	<0.0001	2.30	0.0159	1.35	0.2109
Fall 1996	7.31	<0.0001	1.39	0.1953	1.22	0.2946

Analysis and response variables are as in Table 1.

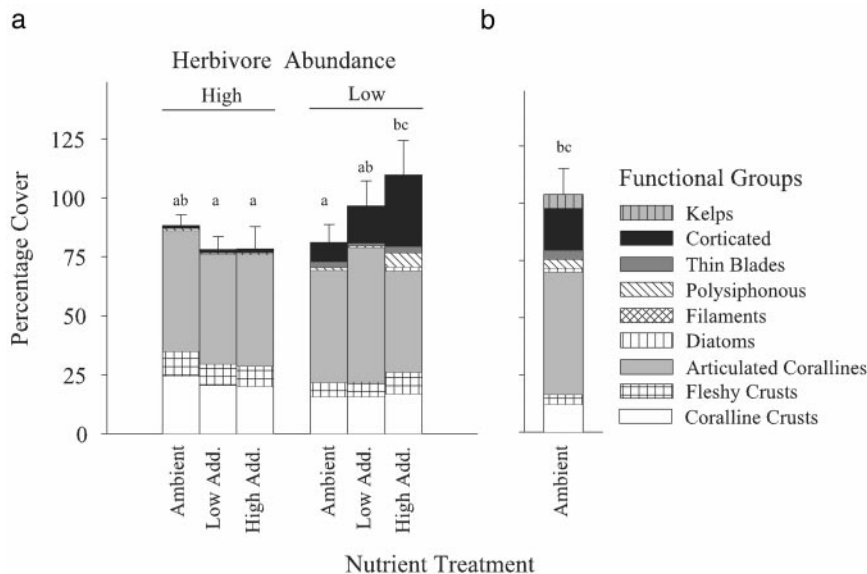


Fig. 3. Abundance of macrophyte functional groups. (a) Total percentage cover of macrophytes (+SE) with average cover of each functional group stacked within each bar ($n = 6$ for each treatment except for the high herbivore biomass, ambient nutrient treatment where $n = 12$). Total percentage cover is linearly related to total macroalgal biomass (32). See Table 1 for statistical analyses of functional group abundances. (b) Macrophyte abundance at a more wave-exposed site where, under natural conditions, nutrients were not limiting and herbivore abundance was low (see *Results* for details). Data are plotted as in a. Different lowercase letters above bars indicate statistically significant differences in total abundance (biomass) among treatments. Functional groups were defined by using traits related to anatomical complexity according to the scheme of Steneck and Dethier (35). Anatomical complexity is negatively associated with surface to volume ratios (S:V), mass-specific growth, and nutrient uptake rates but positively associated with resistance to herbivory (35, 68). The functional groups, listed in increasing order of anatomical complexity, included the following species (69). Diatoms: *Isthmia nervosa*, *Navicula* sp.; filaments: *Cladophora columbiana*; polysiphonous/thinly corticated: *Ceramium* sp., *Microcladia borealis*, *Polysiphonia hendryi*, *Callithamnium pikeanum*; thin blades: *Enteromorpha* sp., *Petalonia fasciata*, *Scytosiphon lomentaria*, *Ulva californica*; heavily corticated: *Chondrocantus exasperata*, *Cryptopleura* sp., *Cryptosiphonia woodii*, *Cumagloia andersonii*, *Dilsea californica*, *Halosaccion glandiforme*, *Mazzaella splendens*, *Mastocarpus papillatus*, *Neorhodomela larix*, *Odonthalia floccosa*, *Osmundea spectabilis*, *Prionitus lanceolata*, *Ptilota filicina*, *Schizymenia pacifica*; kelps: *Hedophyllum sessile*, *Laminaria setchellii*, *Nereocystis luetkeana*; articulated corallines: *Bossiella plumosa*, *Calliarthron tuberculosum*, *Corallina vancouveriensis*; fleshy crusts: *Analipus japonicus* (crustose phase), *Leathesia difformis*, *Ralfsia californica*, *Ralfsia fungiformis*, *Ralfsia pacifica*, *Rhodophysemia elegans*; and coralline crusts: *Pseudolithophyllum* sp., *Lithothamnion phymatodeum*, *Lithophyllum impressum*, and the crustose bases of *Corallina*, *Bossiella*, and *Calliarthron*.

we may view possible consequences of global changes in oceanographic climate (i.e., global warming or more frequent El Niños; refs. 21–23 and 54) and the abundance of consumer populations (i.e., overfishing; refs. 4, 5, and 55–58). It appears that subtle changes in nutrient loading can impact the abundance and diversity of macrophytes, especially where herbivore abundance or effectiveness is limited. The convergence of structure in manipulated pools to that observed in natural pools under similar environmental conditions suggests the results are general. Furthermore, it may represent how macrophyte assemblages would change if bulk nutrient loading were altered. When expressed in the common currency of gross new nitrogen loading, a 40% reduction in flow (or mass transport), which is the difference observed between locations in this study differing in wave exposure, is equivalent to the reduction in nitrogen loading associated with a 1°C increase in water temperature (similar in magnitude to what one might expect during El Niño events in this region, or with geographic variation in upwelling; Fig. 2). Based on these results, one would predict that a persistent reduction of nitrogen loading in open-coast upwelling ecosystems would lead to a decline in the total biomass and functional evenness of macrophytes, similar to that observed with reduced wave exposure.

Global climatic change is predicted to alter upwelling regimes and may also affect the ecological performance (17) and geographical distribution (59) of animal species in open-coast marine ecosystems. Marine macrophytes play important roles in coastal ecosystem structure and functioning by providing habitat (60) and food for higher trophic levels (61), and through biogeochemical cycling (30). We know that changes in the abundance of consumers, such as sea otters and urchins, can have profound effects on the

abundance of marine macrophytes and ecosystem structure (56, 61), but we know much less about how variation in nutrient supply influences these ecosystems. The interactions among these factors and how they influence ecosystem function are not easily predicted and merit further attention.

In open-coast ecosystems, studies have shown that variation in upwelling over time is correlated with altered growth and abundance of subtidal kelps (18) and that variation in upwelling over space is correlated with shifts in the abundances of macrophyte and invertebrate functional groups (19, 62–64). The hypothesized mechanism driving both those changes was variation in nutrient supply driven by coastal upwelling, but experimental evidence was lacking. The results of this experiment strongly support the hypothesis and show that relatively small changes in nutrient supply have the potential to alter important properties of open-coast ecosystems, including the total biomass and evenness of macroscopic primary producers.

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