BOTTOM-UP AND TOP-DOWN FORCES IN TIDE POOLS: TEST OF A FOOD CHAIN MODEL IN AN INTERTIDAL COMMUNITY

Karina J. Nielsen[1]

Department of Zoology, Oregon State University, Corvallis, Oregon USA 97331-2914

Abstract. A simple food chain model of community structure was used to evaluate the roles of bottom-up and top-down factors in a rocky intertidal community. Predictions of the model were modified to incorporate known variation in the strength of species interactions and nutrient delivery rates along a wave-exposure gradient. To test the predictions of the model, I manipulated nutrients and consumers in tide pools chiseled into mudstone benches at two sites that varied in degree of wave exposure. The pools were located in the mid-intertidal zone between ~1 and 1.5 m above mean lower low water (MLLW), at Boiler Bay, Oregon, USA. The focal organisms were the benthic macroalgae and mobile invertebrate herbivores that dominate naturally occurring tide pools at this site.

I manipulated nutrient levels and the abundance of herbivores in these tide pools in a fully factorial randomized block design replicated six times at a wave-exposed and a wave-protected site. The experiment was maintained for two years (1994–1996). The abundances of herbivores and macroalgae were monitored in the spring, summer, and fall of each year. I measured primary productivity in the tide pools during the summer.

Herbivores had a negative impact on algal abundance. The total effect of herbivory, and the efficiency of herbivores per se, on algal abundance was lower at the wave-exposed site. Nutrient additions had a positive effect on algal abundance, but this effect was reduced at the wave-exposed site. Nutrients also appeared to increase algal productivity, but only where herbivore abundance was low. Algal abundance patterns were generally consistent with model predictions for bottom-up, top-down, and hydrodynamic effects. In contrast to model predictions, herbivore abundance did not respond to the nutrient treatment.

The decoupling of consumers from resource dynamics is interpreted to be the result of an herbivore preference for noncalcified seaweeds with higher potential growth rates. In wave-protected pools, where nutrients were most limiting and consumers were most efficient, seaweeds with the potential to translate elevated nutrient levels into growth had no effective refuge from consumers. The difference in scale between resource patches (tide pools) and the foraging range of the dominant herbivore, *Tegula funebralis*, may have augmented the ability of this herbivore to virtually exclude fleshy seaweeds from wave-protected pools. Expanding the domain of applicability of food chain models requires the incorporation of consumer preferences, variation in plant growth rates, environmental gradients, and differences in the relative scales of resource patches and foraging ranges of consumers.

Key words: algal productivity; bottom-up; food chain model; herbivory; macroalgae; nutrients; rocky intertidal; seaweeds; tide pool; top-down; wave exposure.

INTRODUCTION

Ecological theory has not always embraced the idea that top-down and bottom-up forces are inextricably linked to produce patterns in community structure. In 1960 Hairston, Smith, and Slobodkin's top-down view of terrestrial community structure provided a simple but elegant theoretical resolution to the historical debate between the proponents of competition vs. predation structured populations, but subsequently spawned debate over the prevalence of bottom-up vs. top-down factors in structuring communities (Fretwell 1977, White 1978, Oksanen et al. 1981, Hunter and Price 1992, Power 1992, Strong 1992, Polis 1994). For

example, Hunter and Price have argued (1992) argued that bottom-up factors necessarily set the stage upon which all biological interactions are carried out, because in the extreme case, without primary producers, there is no community. The basic, Lotka-Volterra type top-down model, modified by Fretwell (1977) and Oksanen et al. (1981) to include variation in primary productivity, predicts that increasing primary productivity will cause the top trophic level in a system to increase in abundance, as will alternate levels below it, but not the intervening levels. Thus, according to the models, primary productivity can influence both the number of trophic levels, and the absolute abundance of organisms on those levels that are controlled by their resources. However, removal of the top trophic level in the system continues to result in the classic trophic cascade,

whereby relative abundances of the remaining trophic levels are reversed.

There are many empirical studies from a variety of habitats that support this relatively simple model of community structure (Estes and Palmisano 1974, Paine 1980, Oksanen 1983, Carpenter et al. 1985, McNaughton et al. 1989, Power 1990, Rosemond 1993, Wootton and Power 1993, Marquis and Whelan 1994, Stiling and Rossi 1997). However, there are also many studies, both theoretical and empirical, that suggest food webs cannot always be simplified into uniform trophic levels (with food chain like dynamics), and that heterogeneity within a trophic level can result in alternative patterns of abundance (Leibold 1989, McQueen et al. 1989, Leibold and Wilbur 1992, Menge et al. 1994, 1995, Brett and Goldman 1997). Polis and Strong (1996) argue that trophic complexity (such as omnivory) is common, and therefore generalizations with respect to trophic levels are unlikely to adequately describe the majority of systems. In contrast, Hairston and Hairston and Hairston (1993) and Hairston (1997) counter that overarching general patterns exist despite the complexity. Ecologists have also suggested that because food chain models are based on the assumption of a closed system, with no immigration or emigration, they do not realistically capture the dynamics of natural systems. In natural systems, the foraging range of predators may far exceed the foraging range of their prey, or basal resources from adjacent habitats may contribute a significant fraction of the diet of primary consumers. For example Power's (1990) study demonstrating trophic cascades in rivers includes a top predator (juvenile steelhead) which spends most of its adult life in the ocean, and stream invertebrates often receive a significant subsidy from terrestrial detritus that can indirectly affect predators (Wallace et al. 1997). Thus although trophic cascades may be observed, mechanisms based on the assumption of in situ productivity are invalid. Polis and Strong (1996) have argued that trophic subsidies from adjacent habitats (e.g., Bustamante et al. 1995a, Polis and Hurd 1995, 1996, Wallace et al. 1997), which effectively decouple feedback between consumers and their resources, may be a common phenomenon.

The physiological or physical harshness of the environment may also affect which factors are important as controlling agents (Menge and Sutherland 1976, 1987, Lubchenco and Menge 1978, Menge 1978, Menge and Olson 1990, Chase 1996). For example, in intertidal or shallow subtidal communities exposed to breaking waves or oscillatory flow, consumers can be inhibited in their movements or reduce their feeding rates as strong wave forces or high water velocities can dislodge them (Lubchenco and Menge 1978, Menge 1978, Kawamata 1998). Simultaneously, the productivity of benthic plants can be physiologically enhanced as high water flow rates increases nutrient delivery rates (Wheeler 1980, Larned and Atkinson 1997) and exposure to breaking waves increases light utilization efficiency for some seaweeds (Leigh et al. 1987, Wing and Patterson 1993). In a terrestrial example, Chase (1996) demonstrates that a physical factor (shade) limits a herbivore's (grasshoppers) ability to consume its resource and results in both decreased survivorship of grasshoppers in the presence of predators and an increase in plant biomass, relative to the same situation without shade.

The examples above point to the need for more empirical work to tease apart the conditions under which simple food chain models apply, in addition to the relative importance of top-down vs. bottom-up factors in shaping the structure and dynamics of communities. Synthetic analyses of the interacting effects of top-down and bottom-up forces have primarily emerged from studies done in freshwater habitats, while similar studies have been rare in both terrestrial and marine systems (Hunter and Price 1992, Menge 1992). However recent experimental research is beginning to advance our understanding in these systems (Wootton 1991, McGlathery 1995, Posey et al. 1995, Stiling and Rossi 1997).

In rocky intertidal habitats, experimental ecology has generated important insights and conceptual understanding about the structure and dynamics of communities applicable not only to marine systems but to terrestrial and freshwater systems as well. However, most of the studies done in rocky intertidal systems have focused on the roles of competition and predation (sensu latu: including herbivory and collectively referred to as top-down factors). Historically, the role of basal resources such as nutrient availability or other factors influencing the level of primary productivity (collectively referred to as bottom-up factors) has received relatively little attention. In addition, although easy manipulation of organisms has been the hallmark of experimental ecology in rocky intertidal systems, the ability to manipulate primary productivity or nutrient levels is clearly limited. Recent research has shown however, that bottom-up factors do vary in ecologically important ways between sites at relatively smaller spatial scales (within a region 10–100s of kilometers) even in intertidal systems (Menge 1992, Bustamante et al. 1995b, Menge et al. 1995, 1997a, b. Investigations of the role of nutrients and productivity in benthic marine systems have primarily utilized natural experiments and/or the comparative approach (Bosman and Hockey 1986, 1988, Birkeland 1987, 1988, Bosman 1987, Duggins et al. 1989, Wootton 1991, Menge 1992, Menge et al. 1994; but see Bosman et al. 1986, McGlathery 1995, Posey et al. 1995, Wootton et al. 1996). The results of these studies generally support the idea that bottom-up forces can be important in influencing the structure of marine communities.

The goal of this study was to evaluate experimentally all of the likely key influences on intertidal macrophytes: the role of nutrients and their interaction with

herbivores, and the physical gradients associated with wave exposure in a rocky intertidal community. Experimental manipulation of nutrients is not easily done along stretches of open coast habitats, but is feasible in small tide pools which provide a useful experimental system (Metaxas and Scheibling 1993). Because pools are isolated from the ocean during low tide periods, nutrients can be manipulated. Tide pools also provide a refuge from desiccation for consumers during low tide, allowing them to continue foraging and feeding during periods when they might not be able to continue on adjacent benches. Thus these pools serve as distinct patches within the habitat that vary from adjacent areas in accessibility and quality of resources. Furthermore, the effects of hydrodynamic forces on nutrient delivery rates and consumer effectiveness can be addressed by experiments conducted simultaneously at locations that differ in their degree of wave exposure.

Communities in natural tide pools at mid- and high tidal heights at sites on the Oregon coast consisted of two functional trophic levels: primary producers (benthic algae) and herbivorous invertebrates such as the snails, *Tegula funebralis* and *Littorina scutulata*, several species of limpets, chitons, and small crabs (K. J. Nielsen, *personal observation* and *unpublished data*). I experimentally manipulated nutrient delivery rates and the abundance of herbivores in a randomized block design, at both a wave-exposed and a wave-protected site. This experimental design allowed me to test the major hypotheses derived from simple food chain models that incorporate both bottom-up and top-down factors. I was also able to include a priori predictions, based on prior knowledge of the impact of physical factors on biotic interactions in wave-swept environments, of how the effects of nutrients and herbivory might differ between sites varying in their degree of wave exposure (Fig. 1). The following predictions were explicitly evaluated:

1) Nutrient enrichment in a two trophic-level system (primary producers and herbivores) will result in (a) increased primary productivity, (b) increased herbivore abundance (specifically biomass through either increased biomass of individuals or aggregation of consumers), and (c) no increase in the abundance (biomass) of algae;

2) Nutrient enrichment in a single trophic level system (herbivores excluded) will result in increased primary productivity and abundance (biomass) of algae;

3) Nutrients will be more limiting to algal growth at the wave-protected than the wave-exposed site because of the relative differences in flow rates (and thus nutrient delivery rates) and;

4) The effectiveness of herbivores in controlling algal abundance (biomass) will decline with increasing wave exposure due increased physical stress (e.g., wave forces, oscillatory flow).

METHODS

Description of field site

Boiler Bay is located 20 km north of Newport on the central coast of Oregon, USA (44°50′ N, 124°03′ W). Both the ecology and nearshore oceanography of this site are well known (Turner 1983*a*, *b*, Gaines 1984, Menge 1992, Menge et al. 1993, 1994, 1995, 1997*a*, *b*, van Tamelen 1996). Boiler Bay consists of a series of small coves and benches composed of mudstone sheltered to the south by the large cliffs of Government Point, and to the north by a complex of more wave-exposed reefs made up of basaltic and conglomerate rock. The tide pools used in this study were located on a gently sloping mudstone bench divided by narrow channels. I chose two sites within a small cove to represent the two extremes of the wave-exposure gradient that extends from landward to seaward across the bench.

The low zone at the study site is dominated by diverse beds of algae and surfgrasses and beds of urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) in the low intertidal and shallow subtidal zones. Large mobile invertebrates found in the channels include the predatory seastars, *Pisaster ochraceus* and *Pycnopodia helianthoides,* and the herbivorous gum-boot chiton, *Cryptochiton stelleri. Cryptochiton* and *Pycnopodia* are both abundant at this site but are rarely found above the height of the channels, while the intertidal predator *Pisaster ochraceus* is relatively rare (Menge et al. 1994, Navarrete and Menge 1996). The walls of channels surrounding the wave-exposed mid-intertidal benches are sharply zoned from bottom to top: urchins at the bottom, large anemones (*Anthopleura xanthogrammica*) in the middle, a broad band of algae on the upper portion, and a relatively bare zone around the perimeter of the bench surfaces. Mussel beds generally dominate the central, horizontal portion of the benches although the softness of the mudstone in some places is a likely impediment to mussel attachment, and probably contributes to the patchiness of the mussel bed on these benches.

Tide pools at this site are naturally abundant in the soft, rapidly eroding mudstone benches, and have been described by van Tamelen (1996). Major space occupiers include: articulated coralline algae (*Corallina vancouveriensis*, *Calliarthron tuberculosum,* and *Bossiella plumosa*), a diverse group of fleshy red seaweeds (primarily *Mazzaella splendens*, *Odonthalia floccosa*, *Prionitis lanceolata*, *Cryptosiphonia woodii*, and *Dilsea californica*), coralline crusts, and red and brown fleshy crusts (van Tamelen 1992, 1996; K. J. Nielsen, *unpublished data*). Distinct zonation patterns often exist from the top to the bottom of the pools as a result of scour by cobbles and gravel, resulting in bare space toward the bottom of the pools, crustose algae in the midzones, with erect forms most abundant toward the top (van Tamelen 1996). The turban snail, *Tegula fu-*
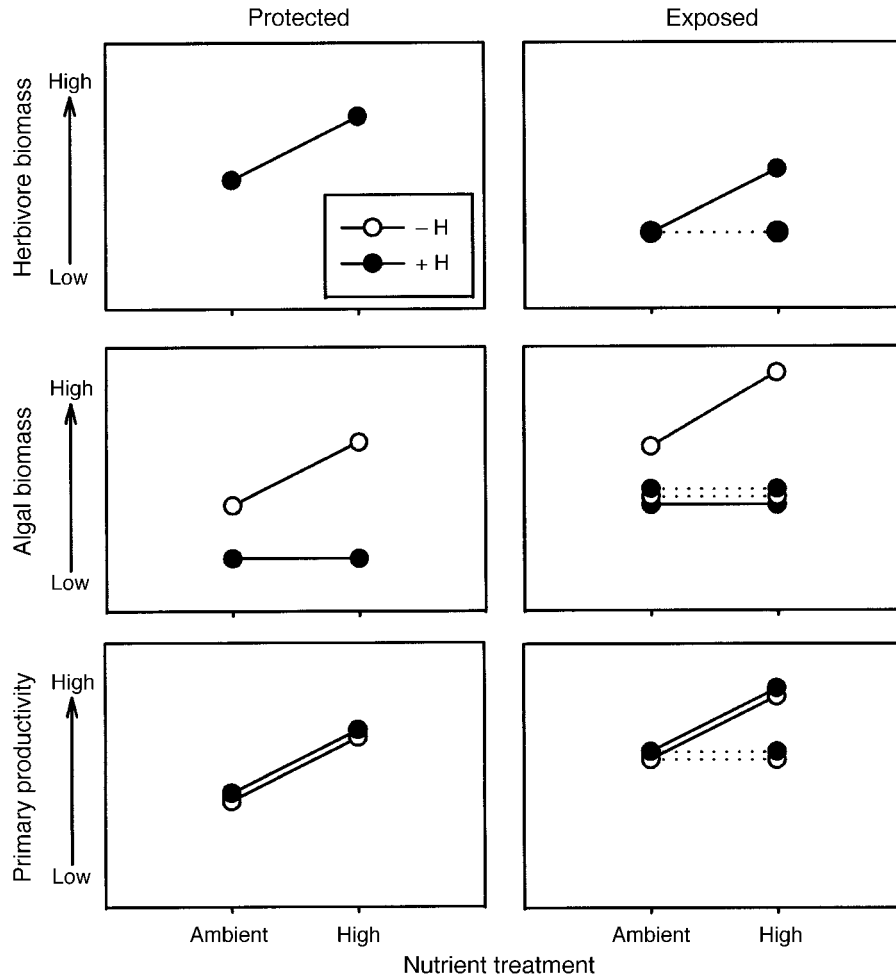
FIG. 1. Predicted effects of increasing nutrients and reducing the abundance of herbivores in a two-trophic-level system. The predictions were based on food chain models but were modified to include hydrodynamic effects on both consumer foraging efficiency and nutrient delivery rates. Nutrient delivery rates were predicted to be lower in wave-protected sites than in wave-exposed sites; hence the potential for limitation of algal growth is greater in wave-protected sites. Hydrodynamic forces were predicted to limit the foraging efficiency of consumers in wave-exposed locations. Herbivore reduction is indicated by −H; the treatment with herbivores left at natural abundances is indicated by +H. Solid lines indicate predictions based on food chain models; dotted lines indicate the maximum predicted change in those predictions due to the modifying effects of hydrodynamic factors.

nebralis, was very abundant in wave-protected pools, while limpets (*Lottia* spp.) were far more prevalent in wave-exposed pools (K. J. Nielsen, *unpublished data*).

Experimental design

In August 1994, I used a jackhammer to chisel 84 bowl-shaped tide pools (mean ± 1 SE; surface diameter, 40.1 ± 0.3 cm; depth, 15.8 ± 0.2 cm; and volume, 11.5 ± 0.2 L) into haphazardly chosen mudstone benches at Boiler Bay. Creating a uniform set of new tide pools of equivalent age and dimensions reduced the problems of historical and physical differences among natural pools. The tide pools were made between +0.97 and +1.63 m above mean lower low water. Six replicate blocks of seven tide pools each were established at each wave exposure. To test predictions

of the model I established three levels of nutrient treatment (ambient, low, and high nutrient flux) and two herbivore treatments (ambient and reduced abundance hereafter referred to as +herbivores and −herbivores, respectively) in a fully factorial design, including appropriate manipulation controls (Fig. 2).

Herbivore abundance was manipulated using a combination of methods. Limpets and chitons were prevented from crawling into pools by barriers of Z-spar marine epoxy putty (Seattle Marine, Seattle, Washington, USA) coated with copper based antifouling paint. Juvenile recruits settling out from the water column were manually removed during each seasonal census. Some herbivores (e.g., *Tegula funebralis*) were not deterred by paint barriers but were excluded by translucent plastic mesh (1/4″ Vexar mesh; Norplex, Kent,
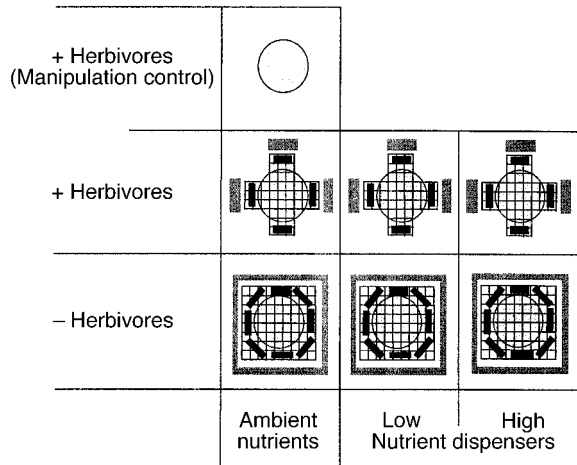
FIG. 2. Experimental design. Three nutrient treatments (ambient nutrients, low, and high) were established using nutrient dispensers attached to the bottom of the pools. Herbivores were excluded using a combination of mesh and copper-painted barriers. Pools where herbivores were free to enter had broken barriers and mesh with openings cut into it. A single unmanipulated pool was included to assess artifacts, if any, from the manipulations. Six replicates were established at both wave-exposed and wave-protected sites in a randomized block design. Each treatment was represented once in each block. See *Methods* for details.

Washington, USA) placed over the tide pools and affixed to the rock using Plexiglas washers and stainless steel screws. I used two methods to control for potential artifacts of the herbivore exclusion while allowing herbivores to freely enter the +herbivore pools. To allow limpets and chitons to enter, partial barriers were painted around pools. To allow *Tegula* to enter, mesh with appropriate sized openings cut into it were placed over the same pools. Although the mesh was made of a translucent plastic, it did reduce incident light below natural levels. I measured photosynthetically active radiation (PAR) ~2 cm below the mesh with a 2π sensor attached to a quantum meter (Li-Cor model numbers LI-192SA and LI-189, respectively; Li-Cor, Lincoln, Nebraska, USA). The mesh reduced PAR by 27.7 $\pm$ 1.5% (mean $\pm$ 1 SE, $n = 10$) when it was dry but by only 14.6 $\pm$ 1.8% ($n = 10$) when under water. The mesh was installed in November 1994; the paint barriers were completed in April 1995.

Nutrient delivery rates were manipulated via nutrient dispensers installed in the pools. Dispensers were fashioned from capped and perforated pieces of PVC pipe (3 cm diameter, 12 cm long) lined with plastic window screen to retain Osmocote (Scotts-Sierra, Marysville, Ohio, USA) controlled-release fertilizer granules (14-14-14 formulation: organic resin coated granules of ammonium nitrate, ammonium phosphate, calcium phosphate, and potassium sulfate [8.2% ammonium, 5.8% nitrate, 14% phosphoric acid, 14% potash]). The granules control nutrient release rates via an osmotic gradient that is set up across the resin layer. Dispensers

were fastened with plastic cable ties to stainless steel eyebolts in the bottom of the tide pools. Three nutrient treatments were established: ambient nutrient flux, dispensers with no fertilizer granules where nutrient concentrations fluctuated as they naturally would, for example, in response to upwelling events; low nutrient flux, dispensers with 20 g of fertilizer granules and two 2-mm holes; and high nutrient flux, dispensers with 40 g of fertilizer granules and four 2-mm holes. Nutrient dispensers were placed in tide pools for a period of six weeks during spring and six weeks during summer in 1995 and 1996.

All of the possible treatment combinations were randomly assigned to pools in each of six blocks at both a wave-exposed and a wave-protected site (hereafter referred to as protected and exposed; Fig. 2). In addition, a completely unmanipulated control pool where herbivores entered freely and nutrients were not manipulated was included in each block. In the absence of artifacts from the mesh and nutrient dispenser per se on the response variables examined, this treatment (unmanipulated control) should be statistically indistinguishable from the +herbivore, ambient nutrient treatment (manipulation control). The experiments were maintained for two years (through November 1996). Algal and animal abundances were monitored in spring, summer, and fall of 1995 and 1996. Productivity was measured during summer when algal growth was high and low tides occurred in daylight (low tides occur at night during fall and winter and it was not possible to get high tide measurements).

Measurement of response variables

Algal abundance.—Algal abundance was calculated using visual estimates of percent cover (Dethier et al. 1993). I designed a conical quadrat to fit inside tide pools using a 50 × 50 cm frame of PVC pipe strung with elastic cord across the frame that passed through the midpoint, to create a grid of 16 wedge-shaped sectors (Fig. 3). At the midpoint where all the cords crossed I attached a metal hook. When sampling, the quadrat was centered over the tide pool and the hook was fastened to an eyebolt in the center of the pool bottom. Each sector covered 6.25% of the pool's surface area. Water was siphoned out of the pool prior to inserting the quadrat and pools were refilled with seawater immediately after monitoring.

I visually divided each sector of the quadrat into six approximately equal parts and scored the number of partitions covered by a given species, systematically quantifying each sector within the grid (in the final calculations each partition scored was equal to 1.042%). Cover of canopy-forming species was estimated first and then the fronds were moved aside to estimate cover of turf-forming and crustose species. I also rated degree of layering for canopy species and height for turf species on a scale of 1 to 4 for the entire pool (1 = turf <2 cm tall or a single layer of canopy;
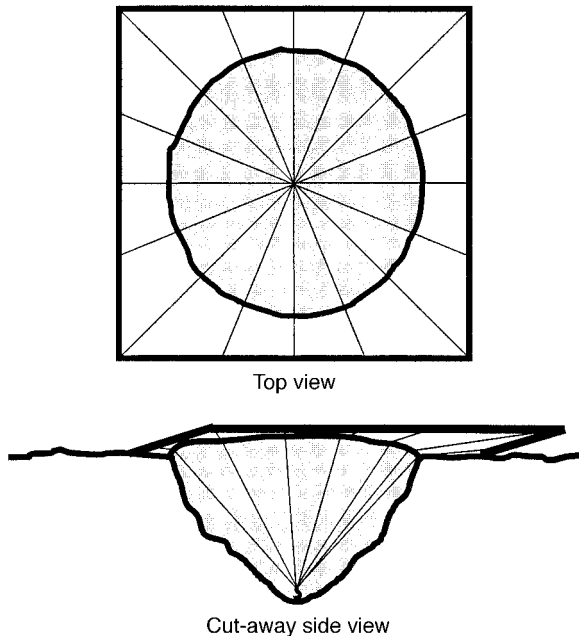
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FIG. 3. Design of conical quadrat used to estimate algal cover. The quadrat is a PVC frame divided into 16 equal sectors by elastic cord with a hook at the center. The quadrat was centered over the tide pool, and the hook was attached to a stainless steel eyebolt fastened to the center of the pool bottom. See *Methods* for details.

2 = turf 2–3 cm tall or a canopy of 2–3 layers; 3 = turf 3–4 cm tall or canopy 4–5 layers; 4 = anything greater). Total cover for each species was defined as the product of the cover estimate and the layer/height rank. Common canopy species included *Mazzaella cordata*, *Dilsea californica*, and *Hedophyllum sessile*; common turf forming species included *Neorhodomela larix*, *Odonthalia floccosa*, *Cryptosiphonia woodii*, *Ceramium* spp., *Corallina* spp., and *Microcladia borealis*).

The relationship between algal cover and biomass (in grams of wet, dry, and ash-free dry mass) was determined in 12 natural tide pools spanning the range of covers of coralline and fleshy algae observed in experimental pools. I visually estimated percent cover as outlined above and then completely harvested the pools. Wet masses were determined after bringing the algal samples into the lab and removing any animals (e.g., gastropods, amphipods, hermit crabs, etc.). Excess moisture was removed from the samples by blotting on paper towels for ~5–10 min before being weighed.

Dry mass was determined by placing each sample into preweighed aluminum foil trays and drying them at 60°C to constant mass. Because dried algae can be extremely hygroscopic (Brinkhuis 1985) samples were cooled in a desiccation chamber and then weighed on an analytical balance with a container of desiccant inside the weighing chamber to avoid uptake of atmo-

spheric moisture. Ash content was determined by combusting the samples in acid-washed porcelain crucibles at 500°C for 4–5 h. Combusted samples were also cooled inside a desiccation chamber before being weighed.

Primary productivity.—In summer of 1995 and 1996, primary productivity (gross) of benthic macroalgae was calculated for each tide pool by measuring oxygen production both in the light (includes both primary production and community respiration) and in the dark (community respiration only). Because making productivity measurements required both good weather conditions and extreme low tides it was not possible to measure productivity in all 84 tide pools. Instead I randomly selected three blocks out of the six available from each wave exposure to use for primary productivity measurements ($n = 42$). Methods were adapted from techniques used to measure primary productivity in open systems such as shallow coral reef lagoons where isolation of water masses occurs during tidal excursions (Kinsey 1978, 1985). Tide pools were covered with a 50 × 50-cm optically pure piece of Plexiglas for two periods of ~45 min each. During the first interval opaque, black plastic sheeting was clipped to the lids to keep light from entering the pools; in the second interval the plastic sheeting was removed. Oxygen concentration was measured using an oxygen meter (YSI 54A) and probe (YSI 5739) at the beginning and end of each interval (YSI, Yellow Springs, Ohio, USA). Oxygen readings were corrected for temperature (measured using a mercury thermometer) and salinity (measured using a refractometer; Strickland and Parsons 1972). To avoid potential problems with loss of dissolved oxygen via bubble formation and supersaturation (which frequently occurred in the morning by the hour of 1000; K. J. Nielsen, *personal observation*), all primary productivity measurements were made as soon after sunrise as possible and dark measurements were always made prior to light measurements.

Exchange of oxygen between the air and water at the surface of the pools was accounted for by calculating a diffusion constant ($K = 0.089 \pm 0.012$ mg $O_2 \cdot cm^{-2} \cdot min^{-1}$ [mean $\pm$ 1 SE], $n = 3$). K represents a constant for a given wind velocity (Kinsey 1985). I assumed that wind velocity was constant throughout all measurement periods because lids always covered the pools during incubation periods. The contribution of phytoplankton to the productivity measurements of tide pools was assessed by incubating 1-L bottles (both light and dark) of seawater from tide pools for the same time intervals. Because changes in oxygen concentration significantly different from zero were never detectable using this method I assumed that phytoplankton productivity was negligible relative to benthic algal productivity.

I measured the amount of incident photosynthetically active radiation (PAR) during each period that productivity measurements were made to characterize the

light environment at each site. I suspected that there might be significant differences in incident light between the two wave-exposure sites because the wave-protected pools were closer to the cliffs and tall trees located on the shore. However, I did not correct productivity measurements for differences in incident light because I always measured productivity simultaneously for all treatments within a block. This allowed for statistical control of differences in the light environment and other physical variables among blocks (within a given wave exposure) measured on different dates, in addition to differences associated with the spatial layout. I measured PAR at 10–20 min intervals from a fixed location in the approximate center of each block. All measurements were taken on days with weather ranging from full sun to partly cloudy, thus the data represent variation in the light field over both space and time at the two sites during relatively good weather conditions.

Animal abundance.—The density of all macroscopic mobile animals was determined by counting the number of individuals in each pool. The mean (± 1 SE) surface area of the bottom of the tide pools was 0.16 $\pm$ 0.002 m². Small and very abundant mobile invertebrates (e.g., the hermit crab *Pagurus hirsutiusculus,* the snails *Littorina scutulata* and *Lacuna marmorata*, and limpets *Lottia* spp.) were subsampled in two randomly chosen sectors (100 cm² each) of the conical quadrat (see *Methods: Measurement of response variables: Algal abundance*). Limpets of the genus *Lottia* were identified to species when possible for individuals >1 cm. All other invertebrates >1 cm in dimension were also measured. Measurements were carapace width of crabs, maximum diameter of *Tegula funebralis* and *Calliostoma ligatum* or axial length of all other gastropods, length of chitons, and test diameter of urchins. Rare invertebrates <1 cm were also measured. Small limpets (probably juveniles of *Lottia strigatella*, *L. digitalis*, and *L. pelta*) were not measured but classified into two size classes: (1) ≤0.5 cm and (2) >0.5 and ≤1.0 cm. The remaining very abundant, small invertebrates which were subsampled were not measured. The relationship between size, numerical abundance, and biomass (dry mass) was determined by counting, measuring, drying (to constant mass at 60°C), and then weighing all the animals collected from 40 small tide pools used in a prior study (van Tamelen 1992, 1996).

Assessment of treatments and physical gradients

To quantify the gradient in wave exposure, differences in wave forces and water flow were measured in five out of six blocks at each of the two sites. Wave forces were measured using maximum wave-force dynamometers (Denny 1988, Bell and Denny 1994) attached to eyebolts in the rock bench in the approximate center of each block. Dynamometers and flow blocks were deployed during two tide series in May (5 d) and June 1997 (4 d). During that time the maximum wave forces measured over each 24-h period were recorded.

Relative water flow rates between sites were measured using molded blocks of dental chalk (Sutherland 1990, Yund et al. 1991, Menge et al. 1995). A pair of flow blocks was placed in each block, one in the upper half of the tide pool wall (open, "manipulation control" pools were used) and another on the surface of the bench just adjacent to the pool. These flow blocks were also centrally located within the block. Relative flow rates in pools with mesh covers were probably somewhat lower than those measured here, but the effect of the covers on flow reduction was not expected to vary between wave exposures. The flow blocks were dried and weighed before being placed out in the field and again after being retrieved at the end of the series. The amount of chalk dissolved per day for each tide series was calculated and is proportional to the flow over the blocks during that period.

The effectiveness of herbivore removals was assessed by monitoring the number and sizes of herbivores in the removal plots during each census. I also monitored the abundance of mobile carnivorous species, primarily gastropods and juvenile crabs, to see if herbivore manipulations had any influence on their abundance.

The effectiveness of nutrient dispensers was tested both in the lab and in the field. An effective treatment should increase nutrient flux (from the dispenser into the tide pool and to the algae) within the tide pools during low tide. I assumed that during high tide nutrients would be flushed out of the pools, becoming diluted and mixed in the overlying water column as a result of exposure to breaking waves and wave surge. Point samples of nutrient concentrations in the pools at low tide, reflect the equilibrium point between dispenser release and algal uptake rates at any given point in time. As a result they need not necessarily show an increased concentration of nutrients in pools with dispensers if, for example, algal uptake rates match dispenser release rates. Nutrient uptake rates of seaweeds in the relatively small volume of the tide pools were high (Nielsen 1998) and could not be assumed to be negligible, therefore I used three methods to assess treatment effectiveness: (1) field measurements of nutrient concentrations in the pools with and without dispensers to ensure that maximum concentrations were bounded within an ecologically relevant range; (2) lab measurements of "fresh" (i.e., never deployed in the field) dispenser release rates to characterize the flux from high and low dispensers (in the absence of algal uptake); and (3) lab measurements of release rates from previously deployed (in tide pools) dispensers to determine if the release rates changed over time or due to deployment in different water flow environments.

I used standard spectrophotometric methods for seawater samples to quantify the concentration of ammonium, phosphate, and nitrate + nitrite (i.e., cadmium

reduction columns followed by chemical reaction to form an azo dye for nitrate + nitrite; formation of indophenol blue for ammonium, and phospho-molybdate for reactive phosphate [Strickland and Parsons 1972, Grasshoff et al. 1983, Parsons et al. 1984, Wheeler 1985]). Nitrite concentrations are typically very low relative to nitrate concentrations in seawater (Lobban and Harrison 1997, Menge et al. 1997b) and were not considered separately here (nitrate will signify nitrate + nitrite hereafter). Samples were taken with 250-mL opaque HDPE plastic bottles. Bottles for sampling and storage (60-mL HDPE bottles) were acid washed and thoroughly rinsed with deionized water prior to use, and rinsed with sample water before filling with sample. Ammonium concentrations were determined immediately, while samples for measurement of nitrate and phosphate concentrations were stored at −20°C for subsequent analysis.

Field measurements of the nutrient concentrations in tide pools both with and without dispensers were taken over a period of tidal isolation. Samples were taken just as the outgoing tide isolated the pools from the ocean and then again ∼5.5 h later before the incoming tide covered the pools again. The water in each pool was thoroughly stirred prior to taking samples. Dispensers had been placed in the pools the day before measurements were taken. Logistical constraints prevented all the pools from being sampled, so a subset of pools was randomly selected. I sampled a total of 36 pools, with 12 replicates of each nutrient treatment (ambient, low, and high).

I calculated fresh dispenser nutrient release rates in the lab in buckets filled with seawater. Three dispensers of each treatment (ambient [control, no nutrients added], low, and high) were individually placed in plastic buckets filled with 11.5 L of seawater (the same volume as the pools) from the running seawater system and placed in a water table filled with flowing seawater to maintain constant temperature. Seawater from the buckets was repeatedly sampled (six times) over a 5-h period. This is approximately the period of isolation from the ocean experienced by pools at the tidal height where the field experiment was located. The water in each bucket was thoroughly stirred prior to taking samples.

A total of 24 dispensers were deployed in the field for testing. Six low-nutrient and six high-nutrient dispensers were placed in randomly chosen tide pools at both the exposed and protected sites. I collected half of the dispensers, three each of the low and high dispensers from each wave exposure, after they had been in the field for 3 wk and the remaining half after 6 wk in the field. On the same day that dispensers were retrieved from the field I brought them to the lab where I calculated nutrient release rates from each dispenser over a 1-h period (using the bucket method outlined above). I calculated the initial rate of release from the fresh control, low, and high dispensers over the first

hour to compare with dispensers that had been deployed in the field to evaluate changes in release rates over time. Release rates were calculated after correcting (by subtraction) for the concentration of nutrients in control dispensers (these did not change significantly over the duration of the trials for any of the three nutrients (paired t test comparing initial vs. final concentrations of ammonium [$P = 0.69$], phosphate [$P = 0.80$] and nitrate [$P = 0.84$]).

Statistical analysis

Algal biomass, cover and productivity, and animal abundance data (i.e., density and biomass of herbivores) collected on several monitoring periods over two years were analyzed using the multivariate approach to repeated-measures analysis (also referred to as "profile analysis" [SAS 1989b, von Ende 1993, Tabachnick and Fidell 1996]) using the GLM (General Linear Model) procedure in SAS version 6.12 (SAS 1989b). Although the communities in the pools were going through succession, the response variables measured were community level properties, repeatedly measured on the same experimental unit (i.e., the community within each pool). The multivariate technique of repeated-measures analysis, assumes and accounts for some correlation (nonindependence) among the response variables (in the multivariate analysis this is among the times that measurements of algal biomass, etc., were taken). This approach allowed use of all of the data I collected at each time interval in a single analysis (Potvin et al. 1990, von Ende 1993). I used the multivariate approach, even though the univariate approach to repeated-measures analysis is generally more powerful, because the restrictive assumptions for the univariate approach for the structure of the variance–covariance matrix (circularity or sphericity condition; Crowder and Hand 1990, Potvin et al. 1990, von Ende 1993, Tabachnick and Fidell 1996) could not be met in most cases. In all but a few of the analyses done here the circularity assumption was strongly violated (Mauchly's criterion for sphericity; $P < 0.0001$). If this assumption is not met, univariate F statistics are inflated (increasing the probability of a type I error) for within-subject factors and their interactions (i.e., time and time by treatment interactions; SAS 1989b, Crowder and Hand 1990, Tabachnick and Fidell 1996, Zar 1996). It is possible to use adjusted F statistics when this assumption is not met but this is only recommended when violations are moderate (SAS 1989b, Potvin et al. 1990). In the three cases where the assumption was met or not severely violated, the interpretation did not vary between approaches, so in the interest of simplicity I only present the multivariate results.

The statistical model evaluated was a multivariate, repeated-measures, randomized block design with blocks treated as a random factor nested within wave exposure (the effect of wave exposure was tested using

the blocks sums of squares and cross products matrix as the denominator rather than the error matrix; Scheiner 1993). Wave exposure and nutrients effects were treated as fixed factors. Herbivore abundances differed somewhat among replicates within a treatment because some species could not be manipulated, and between wave exposures due to differences in natural distribution patterns between the sites (see *Results*). To account for these differences, I used the continuous variable, herbivore biomass (averaged over the six monitoring periods), rather than a class variable ($\pm$ herbivores), in the statistical model to assess the herbivore treatment. I chose herbivore biomass over herbivore density as I considered it a more appropriate common measure of abundance because of the diversity of species and sizes within the herbivore trophic group. Additionally, herbivore biomass remained relatively constant through time unlike herbivore density (see *Results*). This approach allowed for an evaluation of both the main effect of herbivory and how the effectiveness of herbivores, corrected for the potentially confounding effect of abundance, changed with wave exposure per se.

Manipulation controls (tide pools with partial lids, partial copper painted barriers, and empty nutrient dispensers) were compared to controls (no manipulations) to determine if there were artifacts associated with the experimental manipulations and the responses I measured (presence of such an artifact would complicate extrapolation of the effects of the treatments per se to natural conditions [Underwood 1997:228]). The statistical model used to compare the two controls and test for an artifact was: control treatment + exposure + blocks (exposure) + (control treatment $\times$ exposure) + error = response, for each response variable tested. There was never a statistically significant interaction term nor a statistically significant difference between manipulation controls and nonmanipulated controls ($P > 0.33$ in all cases except for fleshy algae where $P = 0.1202$), indicating there were no major artifacts of the manipulations per se for the response variables examined. To utilize all of the available data and maximize statistical power, control and manipulation control data were pooled in subsequent analyses. Although this results in unequal numbers of subjects per treatment, profile analysis does not require that the number of subjects in each treatment group be equal (Milliken and Johnson 1992, Tabachnick and Fidell 1996). In addition, the general linear model used in the GLM procedure of SAS is appropriate for analyzing unbalanced data sets (SAS 1989*a, b*, Crowder and Hand 1990, von Ende 1993).

Details regarding which factors or interactions were included in the statistical models, and whether or not they were predicted to be significant can be visually assessed by inspection of the theoretical model presented in Fig. 1. Higher order interactions that were not predicted by the theoretical model were initially included in the statistical models to assess the goodness of fit of the predicted model without the interaction (Ramsey and Schafer 1997). When the interaction was not predicted, and there was no statistical evidence to suggest that the interaction existed, the term was dropped from the model (Winer et al. 1991, Ramsey and Schafer 1997). My experimental design was based on a traditional randomized block design, and as such it did not include replication of treatments within blocks, therefore all potential block $\times$ treatment interactions (e.g., the three-way block $\times$ nutrient $\times$ herbivore interaction) could not be statistically evaluated due to insufficient degrees of freedom (Underwood 1997). However I did have enough degrees of freedom to check for potential first order block by treatment interactions for both nutrients and herbivores by initially including block $\times$ herbivore and block $\times$ nutrient interaction terms in the statistical models. There was no evidence to suggest that these treatments varied among blocks in any of the analyses done ($P > 0.30$ for all cases), therefore these terms were dropped from the models.

Regression analysis was used derive equations describing the relationship between measures of algal cover and animal abundance and biomass.

Nutrient release rates from fresh dispensers were characterized using separate repeated-measures ANOVAs for each nutrient. Comparison of dispenser release rates among fresh and field deployed dispensers was analyzed using MANOVA with nitrate, phosphate, and ammonium levels as response variables. A repeated-measures analysis was not necessary for comparing among fresh and field dispenser release rates because the units from each time interval were independently deployed and not sampled repeatedly. In the first analysis, using data on initial release rates (>1 h) for both fresh and previously field-deployed dispensers, I tested for the main effects of time and nutrient level. I could not test for wave-exposure effects in this analysis because there was no wave-exposure treatment for fresh dispensers as they had never been placed out in the field (and logically shouldn't have been if they are "fresh"). To assess the effect of wave exposure I conducted a second analysis using only the data from field deployed dispensers, and tested for the three main effects of time, exposure, and nutrient level. Data were log transformed to control for heteroscedasticity.

Assumptions of normality and homoscedasticity were assessed for every statistical model evaluated above by visual inspection of residual plots and normal probability plots of the residuals. When necessary, data were transformed to meet these assumptions. Data presented in figures are always untransformed means $\pm$ 1 SE.

RESULTS

Wave-exposure gradient

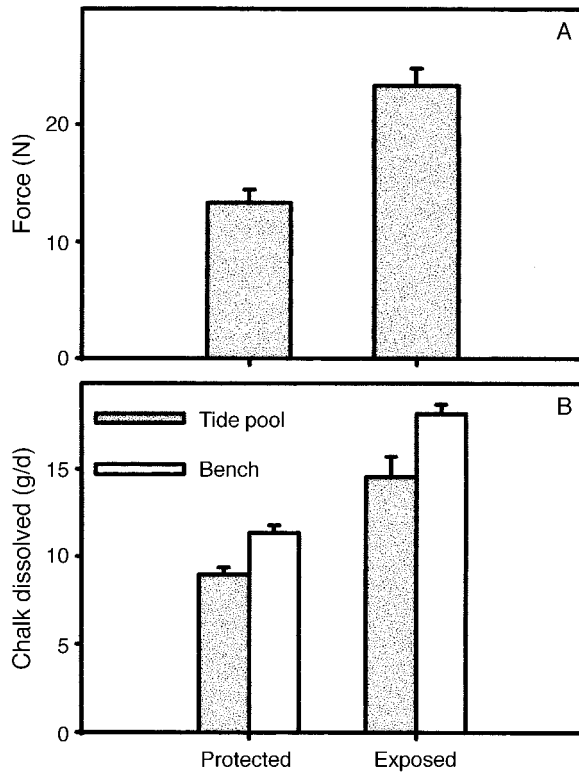The two locations chosen to represent extremes along the wave-exposure gradient within the cove dif-

FIG. 4. Maximum wave forces and relative flow rates. (A) Mean (+ 1 SE; *n* = 35) maximum wave force. (B) Relative flow rates expressed as the amount of chalk dissolved (mean + 1 SE; *n* = 10) from flow blocks. See *Methods* for details.

fered in both maximum wave forces and relative flow rates. Maximum wave forces were 76% greater on benches at the exposed site (Fig. 4a; repeated-measures MANOVA, between subjects, *P* = 0.0005, Wilks' lambda = 3.92, *F* = 31.32, df = 1, 8; log-transformed data). The difference between sites did not vary significantly over the dates sampled (repeated-measures MANOVA, within subjects, *P* = 0.5220, Wilks' lambda = 2.13, *F* = 1.06, df = 6, 3; log-transformed data).

The relative rate of flow over benches and within tide pools was 63% greater at the exposed site (Fig. 4b; repeated-measures MANOVA, between subjects, *P* < 0.0001, Wilks' lambda = 0.1279, *F* = 102.32, df = 1, 14). Flow rates were 22% lower within tide pools relative to adjacent benches (Fig. 4b; repeated-measures MANOVA, between subjects, *P* = 0.0002, Wilks' lambda = 0.3792, *F* = 24.56, df = 1, 14). Both of these effects tended to vary somewhat between the two tide series, although the effects were weak (repeated-measures MANOVA, time × exposure interaction, *P* = 0.0520, Wilks' lambda = 0.7722, *F* = 4.4260, df = 1, 14; time × location interaction, *P* = 0.0450, Wilks' lambda 0.7593, *F* = 4.7554, df = 1, 14). Ocean conditions varied between these two periods. The May tide series was exceptionally calm (K. J. Nielsen, *personal observation*) while the June series occurred during a stormy period (small-craft advisories were issued by the Coast Guard at Depoe Bay, just south of Boiler Bay, on three out of the four days over which measurements were taken).

Treatment effectiveness

Herbivore reduction.—Herbivore manipulations successfully reduced the abundance (total biomass) of herbivores during all monitoring periods (Table 1a). Of

TABLE 1. Herbivore and carnivore abundances.

Season	Protected		Exposed	
	−Herbivores	+Herbivores	−Herbivores	+Herbivores
A) Mean herbivore biomass†				
Spring 1995	8.2 (± 1.0)	49.5 (± 5.1)	3.1 (± 1.3)	17.9 (± 2.3)
Summer 1995	8.9 (± 0.8)	84.0 (± 7.2)	5.9 (± 1.1)	17.4 (± 3.0)
Fall 1995	6.9 (± 0.8)	74.4 (± 5.8)	6.8 (± 1.5)	16.4 (± 2.4)
Spring 1996	6.0 (± 0.6)	63.9 (± 5.6)	4.8 (± 2.0)	17.2 (± 4.0)
Summer 1996	6.3 (± 0.4)	69.5 (± 5.5)	6.6 (± 3.6)	18.2 (± 3.7)
Fall 1996	7.3 (± 1.3)	79.4 (± 8.1)	6.7 (± 1.8)	12.5 (± 1.8)
B) Mean carnivore biomass‡				
Spring 1995	0.2 (± 0.02)	0.2 (± 0.1)	1.0 (± 0.3)	1.9 (± 0.4)
Summer 1995	0.5 (± 0.05)	0.3 (± 0.05)	0.9 (± 0.3)	2.7 (± 0.6)
Fall 1995	0.2 (± 0.1)	0.3 (± 0.1)	1.4 (± 0.4)	2.3 (± 0.6)
Spring 1996	0.2 (± 0.1)	0.1 (± 0.05)	1.6 (± 0.8)	1.8 (± 0.3)
Summer 1996	0.2 (± 0.1)	0.3 (± 0.1)	1.4 (± 0.3)	1.0 (± 0.2)
Fall 1996	0.1 (± 0.1)	0.2 (± 0.1)	1.2 (± 0.2)	1.3 (± 0.3)

Note: All values are dry mass (g)/tide pool ± 1 SE (surface area = 0.16 m²).

† Biomass between +herbivore (*n* = 24) and −herbivore (*n* = 18) treatments is significantly different (*P* < 0.01 by either ANOVA or Welch's AVOVA for unequal variances when appropriate) on all dates within each site (protected and exposed).

‡ Biomass was relatively low and did not differ significantly (*P* < 0.05) between herbivore treatments within each site on any date except for summer 1995 at the exposed site.

all herbivores present, the snails *Tegula funebralis* and *Littorina scutulata*, several species of limpets (*Lottia* spp.), and the hermit crap *Pagurus hirsutiusculus* constitute the bulk of the biomass. Herbivore biomass was greater overall at the wave-protected site, where *Tegula* was more abundant, and reductions created a larger difference in biomass between treatments at the wave-protected than at the wave-exposed site.

Some carnivorous invertebrates were present during the experiment (primarily the whelk *Nucella emarginata*, but other whelks, *N. canaliculata* and *Searlesia dira*, were also present), but they were not very abundant and did not vary significantly with herbivore treatment during any period except summer 1995 when they were more abundant at the exposed site in the +herbivore pools (Table 1b). Although *Nucella* primarily consume mussels and barnacles they will occasionally feed on limpets (K. J. Nielsen, *personal observation*). Presumably the whelks were too small to be impeded by the mesh lids that were attached snugly enough to exclude the larger *Tegula funebralis*, but had small gaps between attachment points where whelks could crawl in. Carnivore biomass was greater at the wave-exposed site.

The other potential predators included seastars and tide pool sculpins. Sculpins, which feed primarily on small crustaceans (e.g., amphipods), did not vary significantly with herbivore treatment. They could pass through the mesh at least while small and were present in 60.0% ($\pm$0.05 [1 SE]) of the pools ($n = 4$ monitoring periods for which I collected data: spring 1995, summer 1995, fall 1995, and summer 1996). Seastars were observed (and removed) near or in the tide pools on only two occasions during the experiment. Both instances occurred at the wave-exposed site, near a deep channel, during a summer warm water period when seastars tend to move higher in the intertidal (Sanford 1999).

Nutrient dispensers.—Nutrient dispensers were effective at raising nutrient levels in the buckets during the lab trials (Fig. 5; repeated-measures MANOVA on log-transformed data, between subjects level effect: nitrate $P = 0.044$, Wilks' lambda = 0.3527, $F = 5.51$, df = 2, 6; ammonium $P = 0.004$, Wilks' lambda = 0.1545, $F = 16.42$, df = 2, 6; phosphate $P = 0.036$, Wilks' lambda = 0.3312, $F = 6.06$, df = 2, 6). Although variability among dispensers was quite high, the means of each treatment were consistently ranked in concordance with treatment levels at every point in time during the trial (Fig. 5). High dispensers were always significantly higher than control dispensers (contrast from repeated-measures ANOVA on log-transformed data, $P \leq 0.01$ for all three nutrients), but only in one case were controls significantly lower than low dispensers (ammonium $P = 0.015$) or high different from low dispensers. The high variance among dispensers may have been due to the initial rapid dissolution of nutrient salts in the occasional cracked or uncoated granule. The rates of release declined over
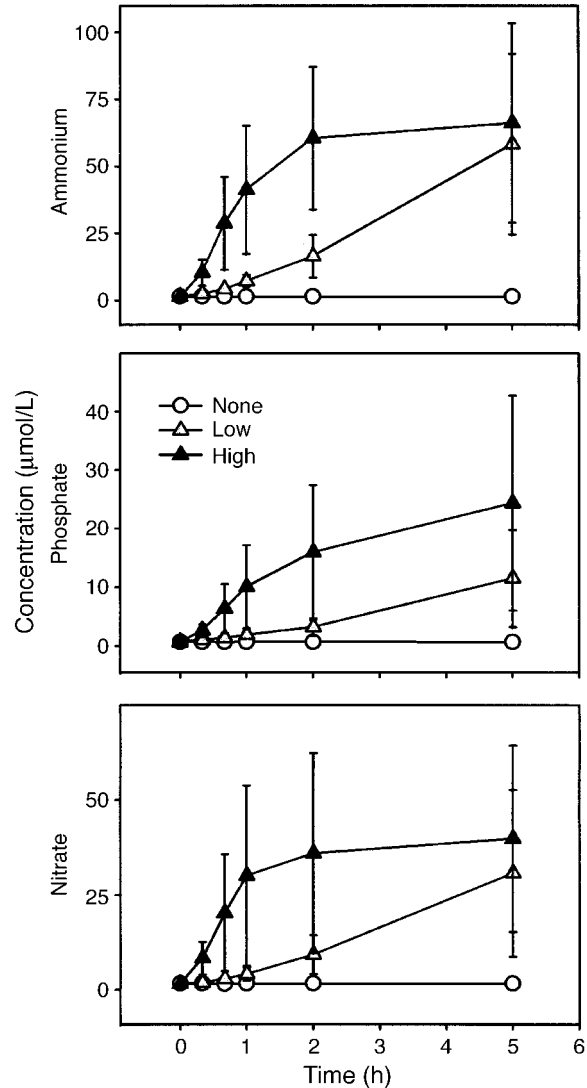

FIG. 5. Rate of release of nutrients from fresh dispensers. The plots show the mean concentration of nutrients ($\pm$1 SE; $n = 3$) over time. Measurements were made in buckets with 11.5 L of seawater and timed-release nutrient dispensers with no nutrients added (none), 20 g (low), or 40 g (high). See *Methods* for details.

the period measurements were taken for ammonium and nitrate in the high nutrient dispensers, as one would expect for an osmotically driven release system (Fig. 5; repeated-measures MANOVA on log-transformed data, within subjects time $\times$ level effect: nitrate $P = 0.027$, Wilks' lambda = 0.0020, $F = 8.45$, df = 10, 4; ammonium $P = 0.014$, Wilks' lambda = 0.0010, $F = 12.10$, df = 10, 4; phosphate $P = 0.161$, Wilks' lambda = 0.0150, $F = 2.86$, df = 10, 4).

In order to evaluate an ecologically relevant range of nutrient levels I attempted to keep maximum nutrient levels experienced by the biota in the pools within the range of concentrations observed in northern Pacific

upwelling regions. The ranges of natural nutrient concentrations observed along the Oregon coast for nitrate, phosphate, and ammonium are 0–30, 0–3, and 0–8 μmol/L, respectively (Fujita et al. 1989, Menge et al. 1997a). In natural, isolated tide pools along the Oregon coast, levels of nitrates and phosphates (relative to levels in the ocean) either stay constant or decline over time due to algal uptake (Nielsen 1998; M. Bracken, *unpublished data*), but ammonium can increase due to the presence of animals actively excreting, often getting as high as 20 μmol/L when invertebrate abundance is high (M. Bracken, *unpublished data*).

Nutrient concentrations in tide pools at the start of the tidal excursion were 25.6 ($\pm$1.8), 2.2 ($\pm$0.1), and 1.2 ($\pm$0.2) μmol/L (mean $\pm$ 1 SE; $n = 12$) for nitrate, phosphate, and ammonium, respectively. Mean nutrient concentrations in tide pools with fresh dispensers, at the end of a typical period of tidal isolation (5.5 h in this case), were 19.3 ($\pm$4.8), 5.0 ($\pm$1.8), 13.3 ($\pm$5.9) μmol/L (mean $\pm$ 1 SE; $n = 12$) with high dispensers, 7.6 ($\pm$2.2), 1.6 ($\pm$0.1), 3.2 ($\pm$0.4) μmol/L (mean $\pm$ 1 SE; $n = 12$) with low dispensers, and 5.9 ($\pm$1.7), 1.2 ($\pm$0.1), 2.6 ($\pm$0.2) μmol/L (mean $\pm$ 1 SE; $n = 12$) in control dispensers, for nitrate, phosphate, and ammonium, respectively, in each case. In the high nutrient treatment the mean concentration of ammonium was higher than that seen in coastal waters. However, it was not higher than what might naturally occur in tide pools with high invertebrate abundances (Jensen and Muller-Parker 1994; M. Bracken, *unpublished data*) or what might be seen in tide pools near seabird colonies (Bosman and Hockey 1986). In addition, it did not exceed ammonium levels thought to be toxic to some macroalgae (gt;30–50 μmol/L; Waite and Mitchell 1972, Graham and Wilcox 2000). Phosphate concentrations in the high treatment were also somewhat above those seen naturally in coastal waters, but as with ammonium, did not exceed levels known to occur in tide pools adjacent to seabird colonies (up to 11 μmol/L; Bosman and Hockey 1986). The mean nutrient concentrations in tide pools with the low nutrient dispensers were elevated relative to the control pools, but fell below the highest levels seen in coastal waters. The levels of nutrients measured here are likely to represent the maximum levels tide pools experienced over the dispenser deployment period because the measurements were made within the first few days of the deployment period, at the end of a period of tidal isolation, and during a period of high ambient nutrient levels typical of an upwelling event along the Oregon coast (e.g., Menge et al. 1997b).

Over the 6 wk that dispensers were deployed in the field, the low-nutrient and high-nutrient dispensers maintained significantly different rates of nutrient release (Fig. 6; MANOVA on log-transformed data, level effect, $P < 0.0001$, Wilks' lambda = 0.3894, $F = 12.55$, df = 3, 24). The mean rate of release for each of the three nutrients was six times greater from the high dispensers than from the low dispensers. There was also a significant reduction in the rate of nutrient release from the dispensers the longer they were in the field (Fig. 6; MANOVA, time effect, $P = 0.0018$, Wilks' lambda = 0.3671, $F = 4.34$, df = 6, 40; log-transformed data). Although rates of release were reduced over time, there was no significant interaction between time and level, indicating that relative treatment differences were similar over the 6-wk period.

Release rates of the field deployed dispensers (at 3 wk and 6 wk) were analyzed to assess how the different flow regimes experienced in the field might have affected dispenser release rates. The mean release rate of dispensers that had been deployed at the wave-exposed site was ~50% (50, 48, and 51% for nitrate, phosphate, and ammonium, respectively) less than those that had been deployed at the wave-protected site (Fig. 6; three-way MANOVA; exposure, week, and level included as factors; exposure effect $P = 0.0180$, $F = 4.59$, df = 3, 15, log-transformed data). This suggests that the higher flow rates at the wave-exposed site (during high tides) depleted the dispensers of nutrients faster than at wave-protected sites, resulting in lower release rates over time than those that had experienced the lower flow regime at the protected site. This makes sense when one recalls that the release rate is osmotically driven in this system. While the effect of level remained significant in this analysis ($P < 0.0001$, $F = 23.31$, df = 3, 15), the effect of week did not ($P = 0.1336$, $F = 2.17$, df = 3, 15). None of the higher order interaction terms were statistically significant. The apparently contradictory result of a significant time effect from the first analysis and the nonsignificant result here, suggests that most of the change in rate of release occurred sometime during the first three weeks of deployment.

Experimental effects

Algal abundance.—The relationship between total algal cover and biomass of multiple-species samples, including both calcified and noncalcified algae, was best described using ash-free dry mass as the measure of biomass (ash-free dry mass [g] = 7.00 + 0.43 × percent cover, $P = 0.001$, $R^2 = 0.72$, $n = 11$; see the Appendix, Fig. A1). This relationship was used to calculate total algal biomass from visual estimates of total cover. Although there was a significant relationship between cover and wet mass ($P = 0.016$, $n = 12$) it only explained 46% of the variance. There was little evidence of a relationship between cover and dry mass ($P = 0.145$, $R^2 = 0.20$, $n = 12$); this is most likely because calcified algae remain quite heavy once dried due to the high $CaCO_3$ content of their thalli relative to fleshy seaweeds.

Algal biomass generally increased over time but there were seasonal trends superimposed on this pattern (Fig. 7; Table 2). Treatment effects were complex, the effect of herbivory varied with wave exposure and
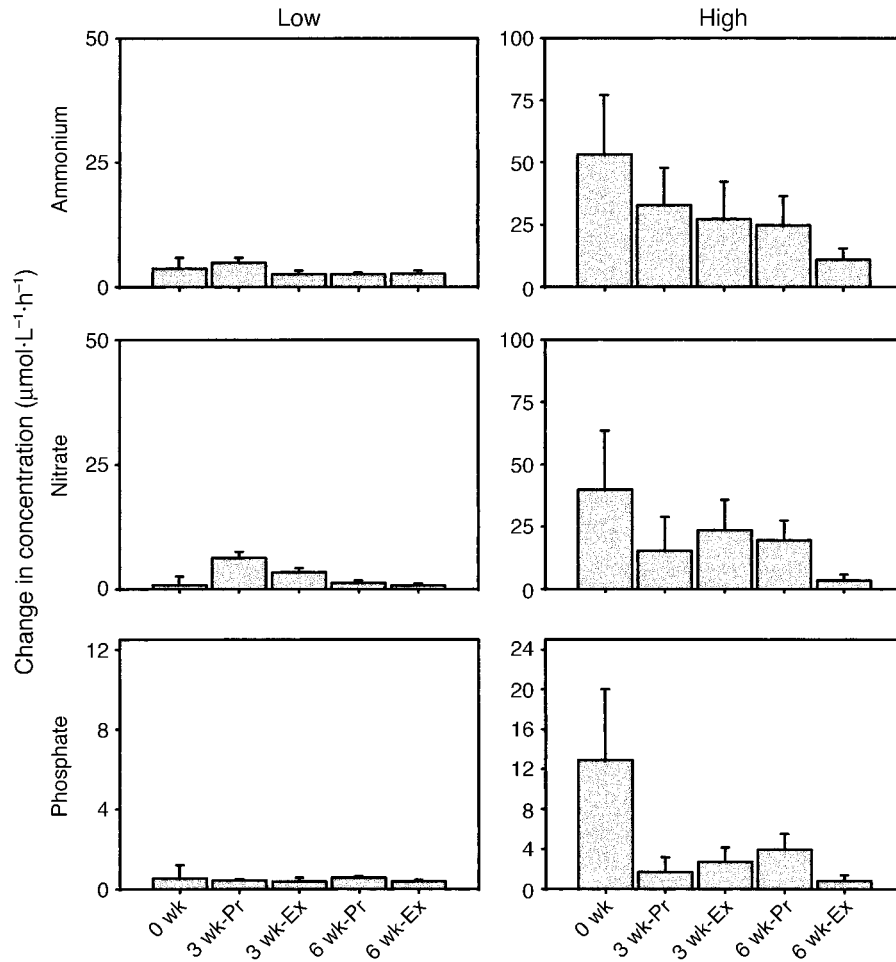
FIG. 6. Release rates from field deployed dispensers. Three dispensers of each type (low and high) were placed in tide pools at both exposed (Ex) and protected (Pr) sites for either three or six weeks. Release rates were calculated in the lab. Data from 0 wk were calculated from fresh dispenser trials shown in Fig. 5. Data are mean release rates (+1 SE; $n = 3$). Note the doubling of scale between Low and High graphs. See *Methods* for details.

changed over time while nutrient effects also varied with wave exposure but did not vary significantly over time (Table 2). A herbivore × nutrient interaction is predicted by simple food chain models, however, by incorporating wave-exposure effects into the model, alternate outcomes were anticipated (Fig. 1). Wave exposure was predicted to have a negative impact on herbivory and nutrients were predicted to be more limiting at the wave-protected site. At the wave-protected site algal biomass appeared to be a function of both bottom-up and top-down factors. Substantial increases in biomass were apparent when nutrients were added to herbivore removal pools (Fig. 7). At the wave-exposed site neither herbivory nor nutrients exhibited a consistent pattern (Fig. 7). Total algal biomass also varied significantly among blocks and over time (Table 2).

I examined the response of calcareous and fleshy algae in separate analyses to determine if the relative abundances of seaweeds morphologically defended from herbivory vs. those that are not had shifted, an

effect that might not be apparent when only considering total biomass. In addition to the effects of morphological defenses per se, the change in nutrient availability may have altered the competitive balance between algae with opposing resource allocation strategies (Coley et al. 1985, Bazzaz et al. 1987).

Coralline algae did not respond in a clear and consistent way to either herbivory or nutrient manipulations (Fig. 8; Table 3). Predictably biomass increased over time, however other strong, consistent effects were not apparent in spite of a significant time × herbivore × exposure interaction (Table 3). There was a slight tendency for coralline algal cover to be greater where herbivores were abundant at some times (Fig. 8). There were also significant differences in cover of coralline algae among blocks that varied with time (Table 3).

In contrast to the response of coralline algae, fleshy algae showed a strong pattern of response to treatments (Fig. 9). Herbivores had a large impact on algal abun-
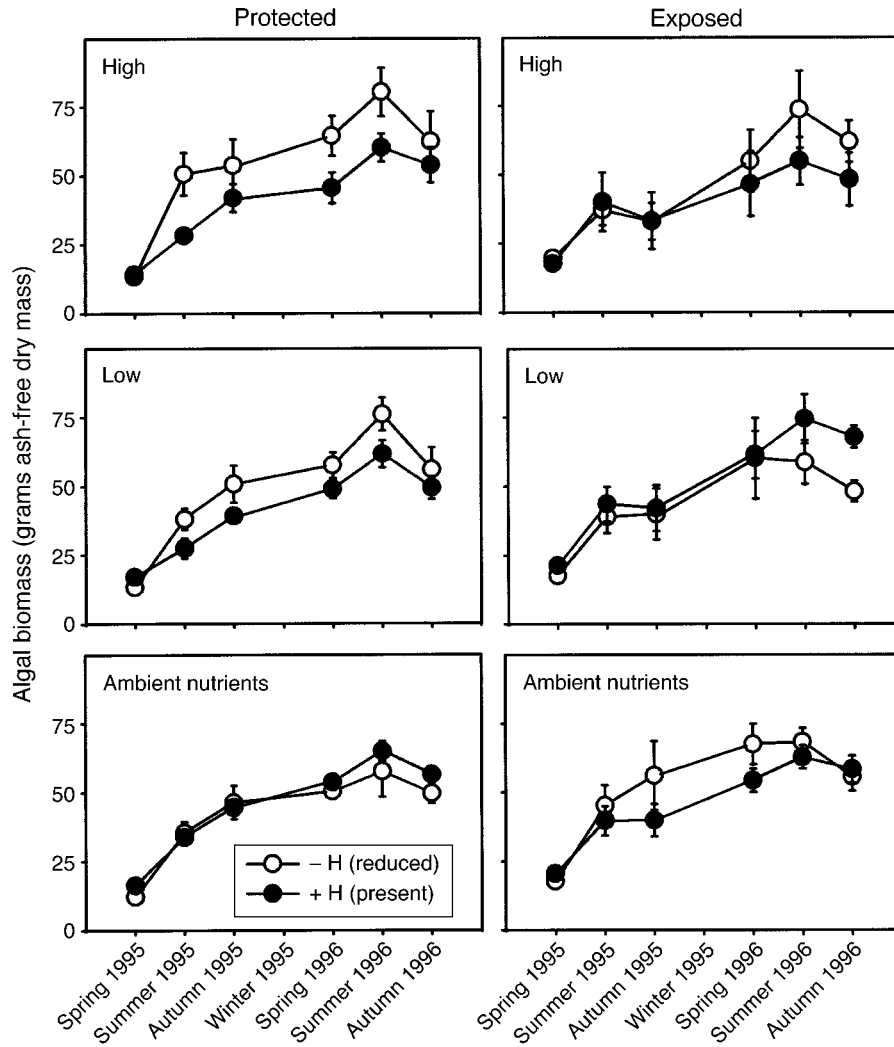
FIG. 7. Algal biomass. +H, herbivores present at natural levels; −H, herbivores reduced. Nutrient treatments are indicated as ambient nutrients, low, and high; exposed and protected sites differ in degree of wave exposure. Data are means (±1 SE) per tide pool (surface area of tide pool bottom = 0.16 m²), for each treatment (n = 6 for all treatments except for the ambient nutrients, +H treatment, where n = 12 due to pooling of manipulation controls with controls). See *Methods* for details.

dance that changed with wave exposure and over time (Table 4). Nutrients also had strong effects overall, but there was some evidence to suggest that this effect did vary to somewhat between wave exposures and with the abundance of herbivores (Table 4). The combined effects of both herbivory and nutrients was greatest on fleshy seaweeds at the wave-protected site (Fig. 9). Averaged over time, fleshy algae were almost four times more abundant when herbivores were removed from wave-protected tide pools but increased by <20% in wave-exposed tide pools. The effect of herbivory was greatest during summers at the wave-protected site and had little effect at the wave-exposed site until the second year of the experiment (Fig. 9; Table 4). In the absence of herbivores, nutrient additions increased the abundance of fleshy algae by 16% and 67% for the low and high treatments, respectively, compared to ambient

nutrient conditions. Seasonal trends in abundance were also apparent with fleshy seaweeds reaching peak abundance during summer of both years (Fig. 9). The abundance of fleshy seaweeds differed among blocks but this effect was not consistent over time (Table 4).

Primary productivity.—Primary productivity (mg $O_2 \cdot cm^{-2} \cdot min^{-1}$) of tide pool algae generally mirrored patterns of algal abundance (Figs. 7 and 10). At natural abundances herbivores reduced mean algal productivity by 38% in 1995 and 19% in 1996 relative to pools where they had been removed, but this effect was not statistically significant (P = 0.1107, Table 5). Nutrients appeared to increase algal abundance in pools where herbivores had been reduced (Fig. 10), the mean percent increase in productivity was positively correlated with nutrient levels (21%, 41% and 88% for ambient, low, and high nutrient treatments, respectively), but

TABLE 2. Results of repeated-measures MANCOVA of algal biomass (ash-free dry mass [g]) as a function of wave exposure (protected or exposed), herbivory (herbivore biomass), and nutrients (ambient, low, or high) over spring, summer, and fall of 1995 and 1996.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 10	0.9966	0.00	0.9966
Herbivore	1, 62	0.9519	3.13	0.0817
Exposure $\times$ Herbivore	1, 62	0.9954	0.29	0.5928
Nutrient	2, 62	0.9646	1.14	0.3273
Exposure $\times$ Nutrient	2, 62	0.8848	4.03	0.0225
Herbivore $\times$ Nutrient	2, 62	0.9853	0.46	0.6335
Exposure $\times$ Herbivore $\times$ Nutrient	2, 62	0.9705	0.94	0.3953
Blocks(Exposure)	10, 62	0.3397	12.05	0.0001
Within subjects (change in effect over time)				
Time	5, 58	0.0877	120.65	0.0001
Time $\times$ Exposure	5, 58	0.7995	2.91	0.0207
Time $\times$ Herbivore	5, 58	0.7425	4.02	0.0034
Time $\times$ Exposure $\times$ Herbivore	5, 58	0.7875	3.13	0.0144
Time $\times$ Nutrient	10, 116	0.1572	1.48	0.1572
Time $\times$ Exposure $\times$ Nutrient	10, 116	0.8192	1.22	0.2880
Time $\times$ Herbivore $\times$ Nutrient	10, 116	0.8500	0.98	0.4636
Time $\times$ Exposure $\times$ Herbivore $\times$ Nutrient	10, 116	0.8522	0.97	0.4774
Time $\times$ Blocks(Exposure)	50, 267.9	0.0941	3.64	0.0001

Notes: The analysis is a multivariate repeated-measures analysis (also known as profile analysis) using the continuous variable herbivore biomass (treated as a covariate), rather than a class variable denoting herbivore treatment level, to assess herbivore effects. Mauchly's criterion for homogeneity of variance–covariance matrices was not met ($P < 0.00001$), so only multivariate results are shown. Exposure was tested using the blocks(exposure) sums of squares and cross-products matrix as the error term. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.6736$). See *Methods: Statistical analysis* for details.

this effect was only marginally significantly ($P = 0.0615$, Table 5). However the power of these tests are reduced relative to tests for effects of these factors on algal abundance patterns because it was only possible to make productivity measurements on half of the available replicates (see *Methods*). The total effect of herbivory appeared to be somewhat greater in wave-protected pools than wave-exposed pools (Fig. 10) but once differences in herbivore biomass were accounted for there was no evidence that this effect varied with wave exposure (Table 5). Productivity did increase to a greater extent in wave-exposed than wave-protected pools between the first and second year of the experiment (Fig. 10; Table 5). Productivity also varied among blocks through time (Table 5).

I calculated biomass-specific algal productivity by converting from mg $O_2 \cdot cm^{-2} \cdot min^{-1}$ to mg $C \cdot g^{-1}$ (ash-free dry mass)$\cdot h^{-1}$ using the algal biomass estimates for each pool and appropriate conversion factors. Absolute rates of biomass-specific productivity during low tide were extremely low (ranging from -0.01 to 9.0×10^{-7} mg $C \cdot g^{-1}$ [ash-free dry mass]$\cdot h^{-1}$) and did not vary significantly with any of the treatments of interest (Table 6). There was, however, significant variation over time associated with blocks (Table 6).

The light field (PAR) during productivity measurements was significantly different between exposed and protected sites (Fig. 11). PAR levels were consistently higher and less variable at the exposed site. As mentioned above, the protected site is closer to cliffs with tall trees that cast shadows, especially early in the morning. The greater variability in the light field is probably a result of the flecking of light through leaves and branches of the trees.

Herbivore abundance.—Herbivore biomass was calculated first for each species, and then summed to total biomass per pool, based on seasonal census data of numerical abundance or size and the predictive equations derived from regression analyses of samples collected before the experiments were initiated (*Appendix*, Table A1). Herbivore biomass was significantly greater at the wave-protected site and also appeared to fluctuate somewhat over time at that site, but those fluctuations were not statistically significant (Fig. 12; Table 7a). There was no evidence that herbivore biomass increased with nutrient treatment (Fig. 12; Table 7a). As with algal responses, there was significant variation among blocks that changed over time (Table 7a).

In contrast to the biomass patterns, there was significant variation in numerical abundance of herbivores between wave exposures and with nutrients over time (Table 7b). During the first year herbivores were more numerous in wave-exposed pools but during the second year abundances from exposed and protected pools converged (Fig. 12). The interaction of wave exposure $\times$ nutrient $\times$ time appeared to be the result of a tendency for herbivore numbers to be somewhat greater in the high nutrient treatment, at some times, in wave-
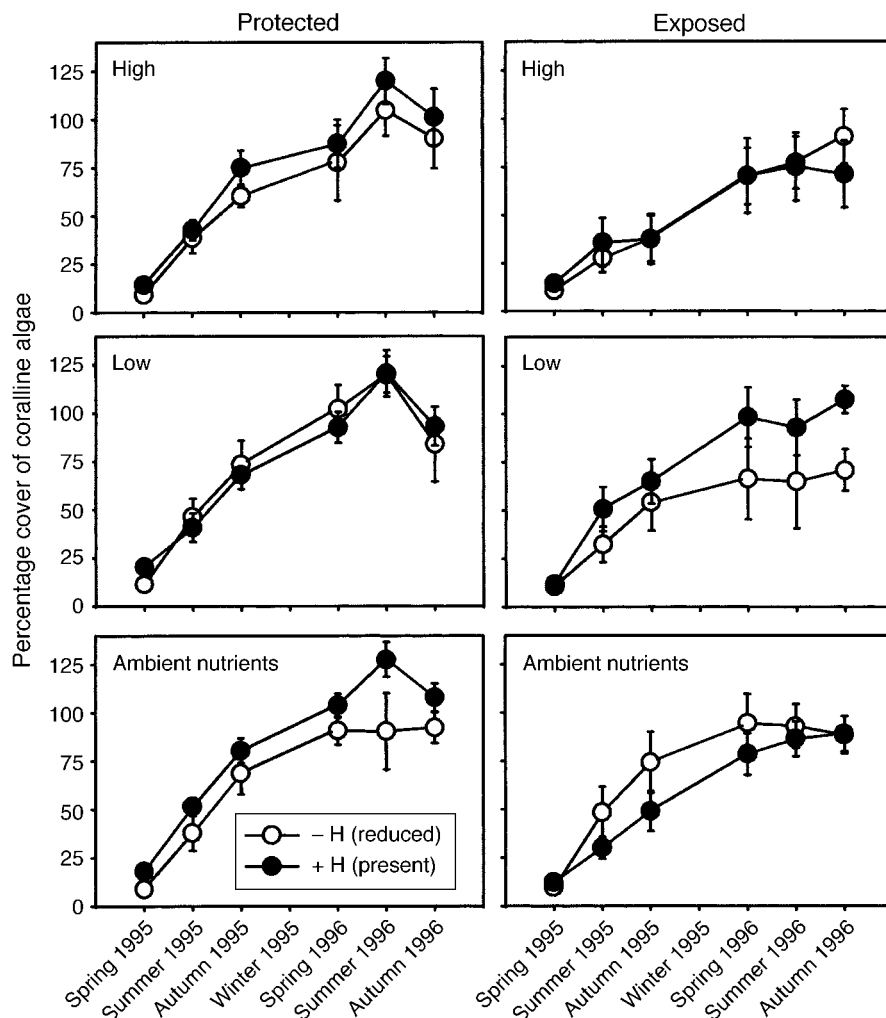
FIG. 8.   Cover of coralline algae. Labels are as in Fig. 7.

exposed pools. Numerical abundance tended to be lowest during the summer for both years (Fig. 12) and also varied among blocks over time (Table 7b).

The large herbivorous gastropod *Tegula funebralis* was much more abundant at the wave-protected site for the duration of the study (averaged over time there were:16.1 ± 0.7 [mean ± 1 SE] *Tegula* in wave-protected pools vs. 1.1 ± 0.2 *Tegula* in wave-exposed pools). However, in wave-exposed pools, small limpets were more abundant during the first year of the study, primarily on bare patches of rock, than in the second year when algal crusts and holdfasts began to dominate the majority of primary space (averaged over spring summer and fall there were 253.9 ± 10.0 limpets <0.5 mm in axial length per pool in 1995 vs. 177.1 ± 8.0 per pool in 1996).

Herbivores that were numerically abundant and could not be manipulated included *Littorina scutulata*, *Pagurus hirsutiusculus*, and *Lacuna marmorata*. Herbivores that were present in very low abundances (<5

per pool for any census and also were not manipulated) included *Hemigrapsus* sp., *Idotea wosnesenskii*, *Pugettia producta*, *P. gracilis*, and amphipods. Amphipods appeared to be less abundant in the tide pools than in comparable patches of algae on adjacent benches (K. J. Nielsen, *personal observation*). It is likely that tide pool sculpins (which were not impeded from entering pools by the mesh lids and were relatively abundant, see *Results: Treatment effectiveness: Herbivore reductions*) kept the abundance of amphipods and other micro-crustaceans low. Although *Lacuna* were occasionally abundant in a few pools, they comprised less than half of a percent of the total biomass where herbivores had not been manipulated, and only 1.3% of the total biomass in the pools where herbivores had been reduced.

Here I only report results of analyses of the numerical abundance patterns of the most common and abundant small herbivores, the littorine snails (*Littorina scutulata*) and hermit crabs (*Pagurus hirsutiusculus*). In

TABLE 3. Results of repeated-measures MANCOVA of coralline algal cover as a function of wave exposure, herbivory, and nutrients.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 10	0.9507	0.52	0.4878
Herbivore	1, 62	0.9903	0.61	0.4385
Exposure × Herbivore	1, 62	0.9999	0.00	0.9555
Nutrient	2, 62	0.9881	0.37	0.6889
Exposure × Nutrient	2, 62	0.9756	0.77	0.4654
Herbivore × Nutrient	2, 62	0.9963	0.11	0.8928
Exposure × Herbivore × Nutrient	2, 62	0.9808	0.61	0.5475
Blocks(Exposure)	10, 62	0.5473	5.13	0.0001
Within subjects (change in effect over time)				
Time	5, 58	0.1489	66.28	0.0001
Time × Exposure	5, 6	0.5231	1.09	0.4495
Time × Herbivore	5, 58	0.6831	5.38	0.0004
Time × Exposure × Herbivore	5, 58	0.6799	5.46	0.0003
Time × Nutrient	10, 116	0.8501	0.98	0.4638
Time × Exposure × Nutrient	10, 116	0.8413	1.05	0.4094
Time × Herbivore × Nutrient	10, 116	0.8590	0.92	0.5212
Time × Exposure × Herbivore × Nutrient	10, 116	0.8195	1.21	0.2892
Time × Blocks(Exposure)	50, 267.9	0.1221	3.14	0.0001

Notes: Mauchly's criterion for homogeneity of variance–covariance matrices was not met ($P < 0.00001$), so only the multivariate results are shown. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.7738$). Remaining details are as in Table 2.

contrast to *Lacuna*, the littorines and hermit crabs (almost always inhabiting shells of *Littorina*), while only 14% of total biomass in the pools with all herbivores present, made up the majority of the biomass (76%) in the herbivore reduction pools.

I analyzed the abundance patterns of these small herbivores across all the pools to see if they varied with any of the factors treated in the experimental design. The numbers of littorines and hermit crabs were combined in this analysis. These small herbivores were generally more abundant in wave-protected pools, especially where the abundance of other herbivores had been reduced (Fig. 13; Table 8). There was also a tendency for them to be slightly more abundant, at some times, where nutrients had been added in the wave-protected pools (Table 8; Fig. 13), but this effect does not appear to be ecologically significant (Fig. 13).

DISCUSSION

Both nutrients and herbivory had effects on tide pool community structure. Their effects were more complex than predicted by simple food chain models. Herbivore abundance patterns were not, however, influenced by the nutrient treatment. Herbivores limited total algal abundance but their effect (both total and per unit biomass) was decreased in wave-exposure pools, as predicted (Fig. 1). The effect of herbivory was most pronounced for fleshy seaweeds. Nutrients affected patterns of algal biomass and productivity but primarily where herbivores were removed. Thus, the prediction based on food chain models that productivity would increase with nutrients both in the presence and in the absence of herbivores was not supported. However, al-

gal biomass was increased by nutrient additions in wave-protected tide pools. This result was consistent with the prediction that nutrients would have a stronger effect on algal biomass and productivity in wave-protected habitats due to the effect of water motion on nutrient delivery rates (Fig. 1; Wheeler 1980, Gerard 1982, Hurd et al. 1996, Larned and Atkinson 1997).

Algal abundance

Total algal biomass was affected by both nutrients and herbivores, in a manner only partially consistent with model predictions (Figs. 1 and 7). Nutrients additions appeared to have stronger effects on algal abundance at the wave-protected site in agreement with the hypothesized mechanism for flow-related nutrient limitation. However, release rate for nutrient dispensers at the wave-exposed site decreased more rapidly than at the wave-protected site. As a result an alternate explanation is that the nutrient treatment at the wave-exposed site was reduced to a sufficient extent that there was no response at the wave-exposed site. Two major functional groups, calcified and fleshy algae, responded differently to these factors (Figs. 8 and 9). The response of coralline algae to both herbivory and nutrients was small and inconsistent. In contrast, fleshy seaweeds, although more susceptible to grazers, clearly responded to nutrient additions and were able to increase in biomass when an escape from herbivory was provided in wave-protected pools. Total fleshy algal abundance was greater at the wave-exposed site over all, but when herbivores were reduced and nutrients added at the wave-protected site, fleshy algal abundance matched that at the wave-exposed site over both years of the
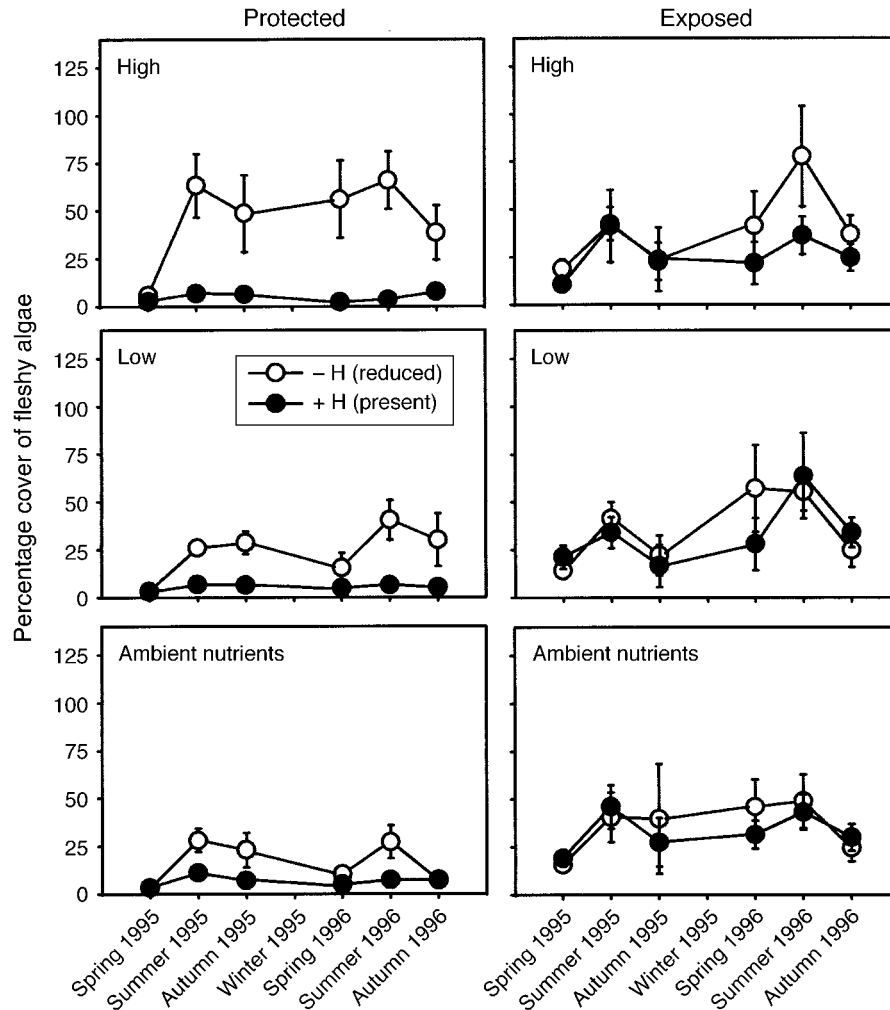
FIG. 9. Cover of fleshy algae. Labels are as in Fig. 7.

experiment. Despite the potential for increased growth of fleshy algae when nutrients were added, addition of nutrients in pools where herbivores were abundant was not sufficient to increase production beyond the rate of consumption. The prevalence of coralline seaweeds in the presence of herbivores, and their lack of response to nutrient additions, suggests that they are incapable of capitalizing on an increase in resources (nutrients) by increasing their growth rate.

The lack of evidence for nutrient limitation of coralline algae in this study is consistent with experimental evidence from the Florida Keys (USA) that demonstrated calcareous macroalgae were less nutrient limited than fleshy species (Delgado and Lapointe 1994). Algae with low growth rates or high nutrient storage capacities may not require either high nutrient levels or frequent pulses of nutrients to persist, while those with higher growth rates and low nutrient storage capacity may not be able to persist without them (Fujita 1985, Pedersen and Borum 1996, 1997). Morphologically undefended, fleshy seaweeds apparently did have the capacity to increase their

growth rate in response to nutrients, but could not persist under strong pressure from consumers.

Competitive dominance hierarchies can change over gradients of productivity or physiological or physical stress (Lubchenco 1978, Fujita 1985). A reversal of competitive dominance between morphologically defended (calcified) algae and fleshy algae under different regimes of herbivory and potential productivity is the hypothesized outcome of such trade-offs (Steneck and Dethier 1994). These results are consistent with a hypothesized trade-off between maximum growth rates and the ability to defend against consumers (Littler and Littler 1980, Lubchenco and Gaines 1981). The differences between coralline and fleshy seaweeds in the extent of their nutrient limitation and resistance to herbivory had opposing and compensatory effects on total algal biomass, dampening the response of total algal biomass to nutrient additions.

The effect of herbivores on fleshy seaweeds was most pronounced in wave-protected pools. This may have resulted from the relatively large foraging range of *Te-*

TABLE 4. Results of repeated-measures MANCOVA of fleshy algal cover as a function of wave exposure, herbivory, and nutrients.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 10	0.8897	1.24	0.2915
Herbivore	1, 62	0.7034	26.14	0.0001
Exposure × Herbivore	1, 62	0.9967	0.20	0.6543
Nutrient	2, 62	0.8491	5051	0.0063
Exposure × Nutrient	2, 62	0.9082	3013	0.0505
Herbivore × Nutrient	2, 62	0.9160	2.85	0.0658
Herbivore × Nutrient × Exposure	2, 62	0.9994	0.01	0.9815
Blocks(Exposure)	10, 62	0.4784	6.76	0.0001
Within subjects (change in effect over time)				
Time	5, 58	0.2979	27.34	0.0001
Time × Exposure	5, 58	0.5274	10.39	0.0001
Time × Herbivore	5, 58	0.8323	2.34	0.0531
Time × Exposure × Herbivore	5, 58	0.8045	2.82	0.0240
Time × Nutrient	10, 116	0.9044	0.60	0.8128
Time × Exposure × Nutrient	10, 116	0.7857	1.49	0.1531
Time × Herbivore × Nutrient	10, 116	0.8977	0.64	0.7741
Time × Herbivore × Nutrient × Exposure	10, 116	0.8406	1.05	0.4049
Time × Blocks(Exposure)	50, 267.9	0.1178	3.21	0.0001

Notes: Mauchly's criterion for homogeneity of variance–covariance matrices was not met ($P < 0.0001$), so only the multivariate results are shown. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.1202$). Data were log transformed prior to analysis. Remaining details are as in Table 2.

gula funebralis, a large, abundant herbivore in wave-protected pools. In South Africa, for example, large patellid limpets are able to keep a wide band of the intertidal zone totally cleared of foliose macroalgae, despite the high intertidal productivity potential in this upwelling region, because of large trophic subsidies from adjacent, subtidal kelp beds (Bustamante et al. 1995*a*).

Algal productivity

Algal productivity patterns generally mirrored those of biomass with greater total productivity where herbivores were reduced (Figs. 7 and 10). Likewise, productivity was increased by nutrient additions only when herbivores were removed. Productivity was not predicted to vary with herbivory, but the increase in productivity with nutrients when herbivores were reduced was consistent with predictions (Fig. 1). Biomass-specific rates of productivity did not change with nutrient additions or herbivory in either wave environment (Table 6). If more productive algae had been able to coexist with their consumers, herbivores might have increased in abundance in response to nutrient additions. Refuges can play a critical role in stabilizing trophic cascades in some systems (Pace et al. 1999). The relatively simple physical structure of the tide pool surfaces may have limited the availability of refuges in space for structurally undefended algae. In contrast, tide pools provide a refuge for consumers from desiccation during low tides, allowing them to continue foraging while those who are emersed on surrounding benches may not. Pools may also attract consumers from surrounding surfaces during low tides further increasing consumer

pressure and reducing the possibility of refuges in either space or time for seaweeds.

Considering the increased algal biomass that was present, it was surprising that there was no evidence of increased biomass-specific productivity rates in response to nutrient treatments—even in the absence of herbivory. This result suggests several alternate, but not mutually exclusive, hypotheses: (1) biomass-specific growth rates were enhanced during an earlier interval perhaps due to seasonal changes in potential productivity; (2) only juvenile/sporeling growth rates were enhanced; or (3) recruitment and survival of sporelings was enhanced in response to nutrient additions.

Productivity of many intertidal species is maximized during summer (Littler et al. 1979, data from California), and is generally maximized in the morning (Lee 1999), so it seems likely that I measured productivity during the optimal season and time of day. However, different species and locations (i.e., California vs. Oregon) have different annual productivity patterns, so this remains difficult to evaluate. Relatively little is known about the ecology and physiology of microscopic algal life history stages but studies of intertidal species do provide some supporting evidence for the other two hypotheses. For example, growth rates of *Fucus serratus* germlings are enhanced with increased nutrients (Creed et al. 1997), nutrient uptake rates of the first year class of a perennial kelp, *Laminaria groenlandica*, are three times greater than both the second and third year classes (Harrison et al. 1986), and survivorship and sexual differentiation of *Lessonia nigrescens* gametophytes are decreased under nitrate and
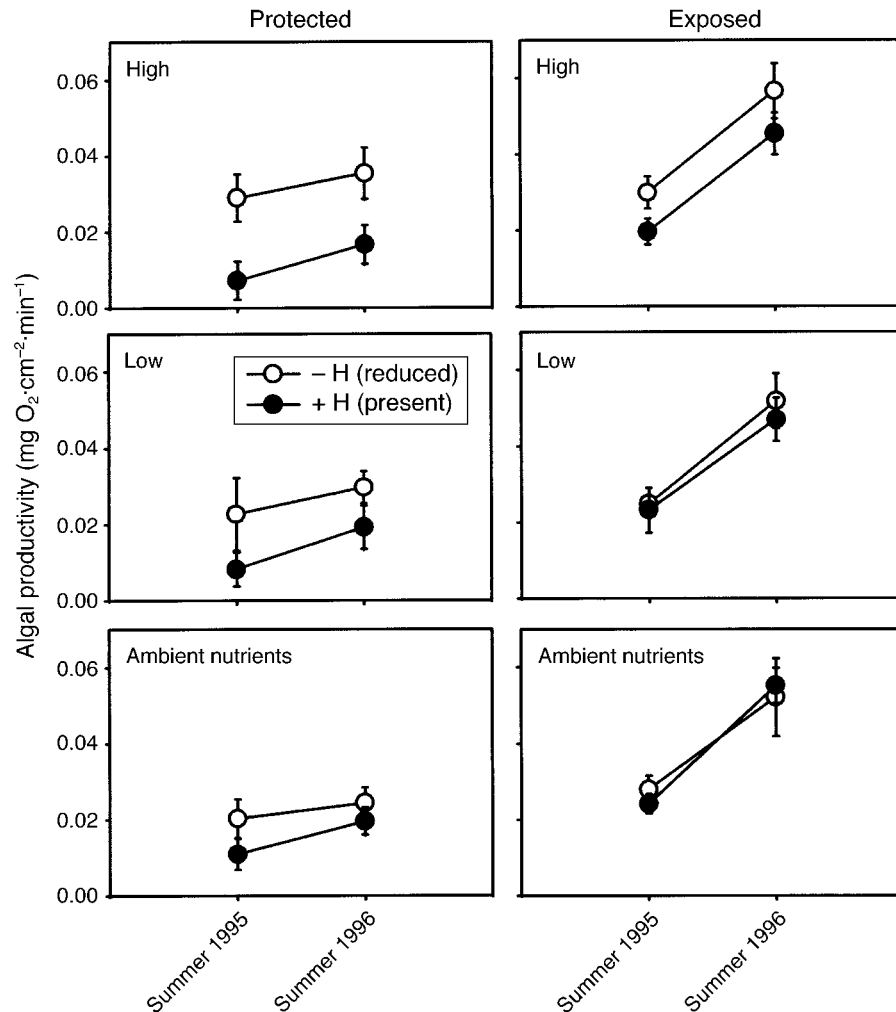
FIG. 10. Primary productivity. Productivity measurements were made only during summer of 1995 and 1996. See *Methods* for details. Labels are as in Fig. 7.

phosphate limitation, respectively (Hoffman and Santelices 1982).

Productivity was greater in exposed than protected pools during the second summer (Fig. 10). Because light levels and water motion were positively correlated with wave exposure at this site, it is possible that either factor contributed to these differences in conjunction with herbivore preferences. The levels of irradiance needed to reach the compensation point (where respiratory needs are just balanced by photosynthesis) for shallow-water seaweeds ranges from 2 to 11 $\mu mol \cdot L^{-1} \cdot m^{-2} \cdot s^{-1}$ (Lobban and Harrison 1997), a level far exceeded (even at the wave-protected site) at all times when productivity measurements were made (Fig. 11). Although the level of incident PAR at the protected site was sometimes below the level necessary to saturate algal growth rates of high intertidal species such as *Fucus* spp., *Ascophyllum nodosum*, *Pelvetia canaliculata*, and *Gigartina stellata* (150–250

$\mu mol \cdot L^{-1} \cdot m^{-2} \cdot s^{-1}$), it was generally not below that necessary for lower intertidal species such as *Laminaria saccharina*, *Chondrus crispus*, and *Codium fragile* (28–94 $\mu mol \cdot L^{-1} \cdot m^{-2} \cdot s^{-1}$; Fig. 11; Lüning 1981). The latter group of species are more representative of the species assemblage in this study as there were no fucoids in any of the tide pools (although two species of *Fucus* occur at this site in the high intertidal zone).

Although the algae in these tide pools were typically species found in the lower part of the intertidal zone and most similar to those indicated above, it is possible that limitation of algal photosynthesis and growth by light was confounded with effects of wave exposure. However, during the first year, when nutrients were added to protected pools where herbivores were reduced, productivity levels matched those of exposed pools (Fig. 10). During the second year productivity was greatest at wave-exposed pools, regardless of treatment. As total algal biomass increased at both sites

TABLE 5. Results of repeated-measures MANCOVA of algal productivity as a function of wave exposure, herbivory, and nutrients during summer 1995 and summer 1996.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 4	0.5776	2.93	0.1624
Herbivore	1, 28	0.9117	2.71	0.1107
Exposure $\times$ Herbivore	1, 28	0.9999	0.00	0.9719
Nutrient	2, 28	0.9190	1.23	0.3064
Exposure $\times$ Nutrient	2, 28	0.8981	1.59	0.2223
Herbivore $\times$ Nutrient	2, 28	0.8194	3.09	0.0615
Blocks(Exposure)	4, 28	0.5450	5.84	0.0015
Within subjects (change in effect over time)				
Time (Intercept)	1, 28	0.4676	31.88	0.0001
Time $\times$ Exposure	1, 28	0.5772	20.51	0.0001
Time $\times$ Herbivore	1, 28	0.9999	0.00	0.9822
Time $\times$ Exposure $\times$ Herbivore	1, 28	0.9946	0.15	0.7000
Time $\times$ Nutrient	2, 28	0.9980	0.21	0.9729
Time $\times$ Exposure $\times$ Nutrient	2, 28	0.9363	0.95	0.3979
Time $\times$ Herbivore $\times$ Nutrient	2, 28	0.9890	0.16	0.8562
Time $\times$ Blocks(Exposure)	4, 28	0.4199	9.67	0.0001

Notes: Because there were only two time intervals, the univariate and multivariate output for repeated-measures analysis are equivalent, and testing for homogeneity of variance–covariance matrices is not necessary (or possible). Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.3306$). The three-way interaction herbivore $\times$ nutrient $\times$ exposure was not theoretically predicted and was not statistically significant ($P = 0.20$); therefore it was dropped from the statistical model. Remaining details are as in Table 2.

(Fig. 7), light may have become more important as a limiting factor. The negative effects of self-shading, as total algal biomass increased, may have been alleviated by the movement of fronds in the greater oscillatory flow experienced by seaweeds in wave-exposed pools (Leigh et al. 1987, Wing and Patterson 1993). This might have allowed pools at the wave-exposed site to support a greater abundance of more productive, fleshy algal species (Fig. 9). Although this is a plausible mechanism, further experimentation is necessary to substantiate this interpretation. Herbivores may also have been less effective at limiting the abundance of algal species with greater productivity potential in wave-exposed pools in part because of the increased availability of light and nutrients, rather than by the direct physical effects of wave exposure.

TABLE 6. Results of repeated-measures MANCOVA of biomass-specific algal productivity as a function of wave exposure, herbivory, and nutrients.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 4	0.5099	3.85	0.1214
Herbivore	1, 26	0.9226	2.18	0.1518
Exposure $\times$ Herbivore	1, 26	0.9958	0.11	0.7432
Nutrient	2, 26	0.9829	0.23	0.7992
Exposure $\times$ Nutrient	2, 26	0.9137	1.23	0.3093
Herbivore $\times$ Nutrient	2, 26	0.9826	0.23	0.7959
Time $\times$ Herbivore $\times$ Nutrient $\times$ Exposure	2, 26	0.9487	0.70	0.5045
Blocks(Exposure)	4, 26	0.7845	1.79	0.1621
Within subjects (change in effect over time)				
Time (Intercept)	1, 26	0.9389	1.69	0.2047
Time $\times$ Exposure	1, 26	0.9939	0.16	0.6927
Time $\times$ Herbivore	1, 26	0.9919	0.21	0.6496
Time $\times$ Exposure $\times$ Herbivore	1, 26	0.9914	0.23	0.6389
Time $\times$ Nutrient	2, 26	0.9338	0.92	0.4103
Time $\times$ Exposure $\times$ Nutrient	2, 26	0.8776	1.81	0.1831
Time $\times$ Herbivore $\times$ Nutrient	2, 26	0.9987	0.02	0.9831
Time $\times$ Herbivore $\times$ Nutrient $\times$ Exposure	2, 26	0.9382	0.86	0.4365
Time $\times$ Blocks(Exposure)	4, 26	0.5976	4.38	0.0077

Notes: Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.3322$). Details are as in Tables 2 and 5.
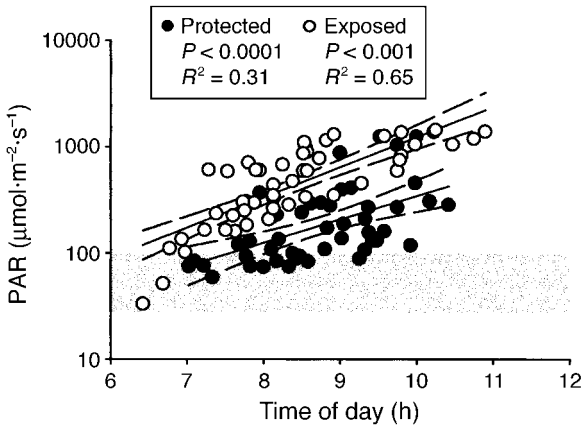
FIG. 11. Light field during productivity measurements. Dashed lines are 95% confidence intervals for regressions; the shaded box indicates the range of light levels known to saturate growth rates for lower intertidal algal species (Lüning 1981).

The absolute productivity values were very low (Fig. 10). This was not entirely unexpected as the conditions in these relatively small-volume pools were not conducive to maximizing photosynthetic rates. Large algal biomass to water volume ratios can have significant negative impacts on photosynthesis through CO_2 and nutrient limitation and high O_2 tension (Littler 1979,

Bidwell and McLachlan 1985). In addition some intertidal algae have been documented to have greater photosynthetic rates out of water than immersed (Johnson et al. 1974) as well as desiccation-enhanced nutrient uptake (Thomas et al. 1987). Other critical factors include shading due to multiple layers of canopy and the absence of water motion in tide pools during low tide (Littler 1979). However these are the natural conditions for this community during low tide and thus representative of realistic rates.

Herbivore abundance

Contrary to model predictions (Fig. 1), the majority of the variation in herbivore biomass was explained by factors associated with wave exposure (Fig. 12; Table 7). A combination of large and small herbivores (mostly *Tegula funebralis*, *Littorina scutulata*, and *Pagurus hirsutiusculus*) dominated at wave-protected sites while smaller herbivores (*Lottia* spp. and *Lacuna marmorata*) were abundant at the wave-exposed site. Temporal variation in herbivore biomass was surprisingly low, especially considering the large changes evident in numerical abundance over time (Fig. 12).

The patterns of change suggest that small herbivores were replaced by larger ones in wave-exposed pools during the second year of the experiment. This transition coincided with an increased herbivore effect, particularly for fleshy algal species (Fig. 9). However, in
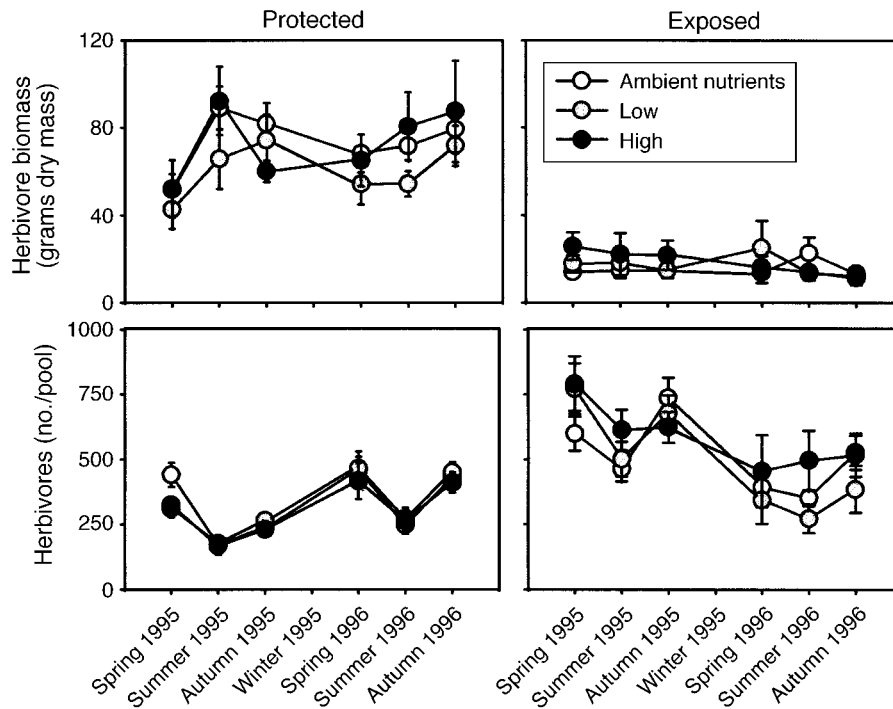

FIG. 12. Herbivore abundance. Data are only plotted for tide pools where herbivores were not excluded. Top panels, total herbivore biomass per tide pool (surface area = 0.16 m²). Bottom panels, numerical abundance of herbivores per tide pool. Data are means ± 1 SE; *n* = 6 for low and high, and *n* = 12 for ambient nutrients due to pooling of manipulation controls and controls.

TABLE 7. Results of repeated-measures MANOVA of herbivore biomass and density (in +herbivore pools only) as a function of wave exposure and nutrients over spring, summer, and fall of 1995 and 1996.

Source	df	Wilks' λ	F	P
A) Herbivore biomass†				
Between subjects (mean effect over time)				
Exposure	1, 10	0.0993	90.73	0.0001
Nutrient	2, 32	0.9750	0.41	0.6668
Exposure $\times$ Nutrient	2, 32	0.9629	0.62	0.5465
Blocks(Exposure)	10, 32	0.6891	1.44	0.2065
Within subjects (change in effect over time)				
Time (Intercept)	5, 28	0.7765	1.61	0.1896
Time $\times$ Exposure	5, 28	0.7024	2.37	0.0648
Time $\times$ Nutrient	10, 56	0.7236	0.98	0.4684
Time $\times$ Exposure $\times$ Nutrient	10, 56	0.5989	1.64	0.1201
Time $\times$ Blocks(Exposure)	50, 131	0.0312	2.99	0.0001
B) Herbivore density‡				
Between subjects (mean effect over time)				
Exposure	1, 10	0.4794	10.86	0.0081
Nutrient	2, 32	0.9756	0.40	0.6735
Exposure $\times$ Nutrient	2, 32	0.9027	1.72	0.1943
Blocks(Exposure)	10, 32	0.3430	6.13	0.0001
Within subjects (change in effect over time)				
Time (Intercept)	5, 28	0.1778	25.90	0.0001
Time $\times$ Exposure	5, 28	0.2266	19.11	0.0001
Time $\times$ Nutrient	10, 56	0.6904	1.14	0.3503
Time $\times$ Exposure $\times$ Nutrient	10, 56	0.3800	3.49	0.0013
Time $\times$ Blocks(Exposure)	50, 131	0.0438	2.58	0.0001

† Mauchly's criterion for homogeneity of variance–covariance matrices was not met ($P = 0.0001$), so only the multivariate repeated-measures analysis is shown. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.2633$). Data were log transformed to control heteroscedasticity.

‡ Mauchly's criterion, although not met, was not severely violated in this case ($P = 0.0217$), so the corrected univariate repeated-measures statistics were examined. These results did not differ in interpretation from the multivariate results, so in the interest of simplicity only the multivariate analysis is shown. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.4492$). Data were square-root transformed to control heteroscedasticity.

the second year of the experiment, juvenile urchins (*Strongylocentrotus purpuratus* <1 cm test diameter) recruited into the exposed pools during the spring and summer (K. J. Nielsen, *personal observation*). They were removed from herbivore-reduction pools, but may have contributed to the increased herbivore effect during the second year of the experiment. The following summer (1997), most exposed pools had two to five small urchins in them (clearly from the previous years' cohort) and apart from coralline crusts there was little algal cover (K. J. Nielsen, *personal observation*). Thus although the foraging efficiency of the snails and hermit crabs was negatively affected by wave exposure during the course of this study, it is likely that this pattern would have changed as urchins, which are more voracious and efficient consumers than gastropods, took up residence (e.g., Paine and Vadas 1969).

Interestingly, removal of herbivores from wave-protected tide pools (primarily the relatively large *Tegula funebralis*) evidently had a positive impact on the abundance of smaller herbivores (*Pagurus hirsutiusculus* and *Littorina scutulata*; Fig. 13). This suggests that

there may have been competition for resources between these two groups of herbivores. The hermit crab, *Pagurus hirsutiusculus*, has been documented to have negative effects on epiphytic diatoms especially at high densities (Ruesink 1998*b*). The growth and productivity of *Odonthalia floccosa*, a common alga in these tide pools, is in turn negatively impacted by heavy epiphyte loads of diatoms, but because they tend to colonize *Odonthalia* late in the summer, after growth and reproduction have occurred, the population effects are small (Ruesink 1998*a*). It is therefore possible that herbivore effects were underestimated in this experiment because of the increase in the abundance of these smaller herbivores in the herbivore removal treatment.

There was some evidence that small herbivores were more abundant in wave-protected pools when nutrients were added. The relatively low abundance of diatoms in wave-protected pools observed during this experiment may have been a result of the relatively high densities of hermit crabs (Ruesink 1998*b*). The effect of these smaller invertebrates on algal biomass and productivity remains unclear, however, since they could
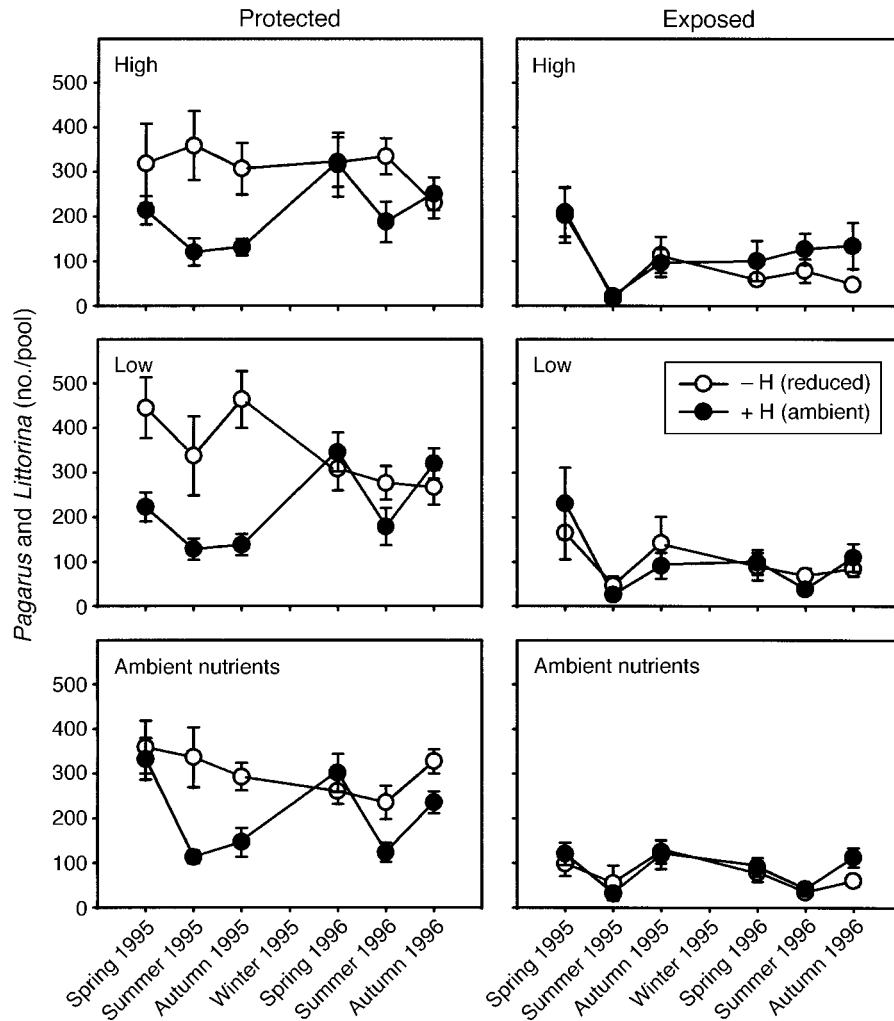
FIG. 13. Numerical abundance of *Littorina scutulata* and *Pagurus hirsutiusculus*. Abundances of other herbivores were manipulated. Labels are as in Fig. 7.

not be manipulated. In a similar experiment where nutrients and herbivores were manipulated on nutrient-releasing clay pot surfaces, Wootton et al. (1996) found that nutrients increased the abundance of micrograzers (chironomid larvae and amphipods) in one year, but not others. However, micrograzers were more abundant when molluscan grazers were reduced, over all three years that the experiments were repeated (1992–1994). They suggest that ocean-wide changes in oceanic conditions generated by the 1992 El Niño were responsible for the change in the micrograzer response to nutrient additions (i.e., they assumed nutrients were limiting during the El Niño year, but not in non-El Niño years). I witnessed similar patterns of abundance among large and small herbivores, but nutrient additions appeared to have had a small influence on abundance patterns during a non-El Niño period (1994–1996).

The contrasting response of smaller vs. larger herbivores during this and Wootton et al.'s (1996) exper-

iments suggests that species interactions varied with spatial scale. In this study larger consumers were free to move between pools and forage on adjacent benches, while smaller herbivores were restricted to foraging inside of a given pool, thus a decoupling of consumer–resource interactions might be expected (Polis and Strong 1996). The large snail, *Tegula funebralis*, was the most abundant herbivore in wave-protected pools, but frequently moved between pools and traveled large distances. Individually marked snails traveled a mean (± 1 SE) of 30.4 (± 5.4) m over a two-week period at this site (J. Whitsett, *unpublished data*). Therefore, at the scale of a tide pool, *Tegula* might be considered a consumer with a trophic subsidy from an adjacent habitat (benches), while for smaller invertebrates the tide pool represents a relatively closed system. Although highly mobile consumers, whose foraging range exceeds the scale of productivity manipulations, are predicted to aggregate in higher productivity patches (e.g.,

TABLE 8. Results of repeated-measures MANCOVA of numerical abundance of small herbivores that were not manipulated during the course of the experiment (littorines and hermit crabs), as a function of wave exposure and herbivore and nutrient treatments over spring, summer, and fall of 1995 and 1996.

Source	df	Wilks' λ	F	P
Between subjects (mean effect over time)				
Exposure	1, 10	0.1569	53.74	0.0001
Herbivore	1, 62	0.9813	1.18	0.2819
Exposure × Herbivore	1, 62	0.9451	3.60	0.0624
Nutrient	2, 62	0.9616	1.24	0.2966
Exposure × Nutrient	2, 62	0.9936	0.20	0.8183
Herbivore × Nutrient	2, 62	0.9993	0.02	0.9781
Exposure × Herbivore × Nutrient	2, 62	0.9966	0.11	0.8997
Blocks(Exposure)	10, 62	0.5834	4.43	0.0001
Within subjects (change in effect over time)				
Time (Intercept)	5, 58	0.6018	7.67	0.0001
Time × Exposure	5, 58	0.7937	3.01	0.0174
Time × Herbivore	5, 58	0.8670	1.78	0.1314
Time × Exposure × Herbivore	5, 58	0.9502	0.61	0.6937
Time × Nutrient	10, 116	0.7104	2.16	0.0249
Time × Exposure × Nutrient	10, 116	0.7013	2.25	0.0193
Time × Herbivore × Nutrient	10, 116	0.7607	1.70	0.0887
Time × Exposure × Herbivore × Nutrient	10, 116	0.7990	1.38	0.1192
Time × Blocks(Exposure)	50, 267.9	0.1138	3.27	0.0001

Notes: The covariate, herbivore biomass, was corrected for this analysis by subtracting the biomass contributed by the littorines and hermit crabs prior to analysis. Mauchly's criterion, although not met, was not severely violated in this case ($P = 0.0215$), so the corrected univariate repeated-measures statistics were examined. These results did not differ in interpretation from the multivariate results, so in the interest of simplicity only the multivariate analysis is shown. Manipulation controls were pooled together with controls as there was no evidence that an artifact of the manipulation caused them to differ from controls for this response variable ($P = 0.3925$). The data were square-root transformed to control for heteroscedasticity.

Nutrient manipulations

The effect of nutrients on marine ecosystems is of fundamental importance to both basic and applied ecological research, however the difficulties associated with experimental manipulation of this factor has limited our understanding of how bottom-up factors influence marine communities. In the extreme, we know from a wealth of observational data, that anthropogenic eutrophication of semi-enclosed bodies of water (i.e., bays, estuaries, lagoons, etc.) is among the most serious and well-documented threats to coastal ecosystems (Vitousek et al. 1997). At a larger scale in the open ocean we also know that El Niño events, or other changes in oceanic climate or upwelling regimes that result in reduced nutrient availability, can have strong influence on the abundance and productivity of many trophic levels ranging from phytoplankton to kelps, zooplankton to pinnipeds, and fish to seabirds (Limberger 1990, Veit et al. 1996, 1997, McGowan et al. 1998, Dayton et al. 1999; Halpin et al., *in press*). At a time in history when humans are increasingly influencing the rates of biogeochemical cycles that can impact marine systems (e.g., nitrogen fixation and its potential to end up in nearshore marine ecosystems; Vitousek et al. 1997, Tilman 1999), the development and refinement of exper-

imental approaches to address the general ecological question, ''how do nutrients influence nearshore marine ecosystems?'' is essential.

Experimental studies of nutrient effects on coastal marine macrophytes or tide pool biota have used a variety of techniques depending on the nature of the experiment or specific question being addressed (e.g., population or community level inquiry; lab, field, or mesocosm system). Typically these have included: incubations in concentrated solutions, continuous flow systems, single or multiple spikes or additions of concentrated solutions, slow-release matrices (e.g., agar), and dispensers of various types. Comparison among these studies is hindered due to differences in the kinds of data researchers report, and to a lesser degree by methodological differences. Some studies, generally among those using slow-release type matrices, do not report nutrient levels experienced by the biota in either manipulated or ambient (control) treatments treatments (e.g., Posey et al. 1995), only indicate composition of the slow-release matrix they used, and in some cases only ratios of nutrients within the matrices (Pedersen and Borum 1996, Wootton et al. 1996). This makes assessment of treatment effectiveness and levels relative to the question of interest difficult to evaluate. While often the question of interest is simply whether or not there is nutrient limitation at all, hence a simple ''+nutrient'' treatment is considered sufficient, many studies use treatment levels that far exceed the ob-

served range for the ecosystem under study (ranging from double to over an order of magnitude greater than the maximum reported; e.g., Harlin and Thorne-Miller 1981, Fujita 1985, Bosman et al. 1986, Lapointe 1987, 1997, Fujita et al. 1989, Burkholder et al. 1992, Coleman and Burkholder 1995, Metaxas and Scheibling 1996, Pedersen and Borum 1996, Miller et al. 1999). This is not unusual nor particular to the study of macrophytes, indeed it is also typically the case in studies assessing nutrient limitation of phytoplankton in marine ecosystems (Downing et al. 1999).

A critical question in evaluating the relevance of any experimental manipulation to natural systems is the degree to which the treatment levels reflect what the organisms under study are likely to experience (Dunham and Beaupre 1998). In this study my goal was to evaluate an ecologically relevant range of nutrient levels. To meet this goal I tried to limit the maximum nutrient concentrations within the tide pools to the maximum levels that might occur naturally within the system and applied the treatment periodically during a time of the year when high nutrient levels occur naturally. There were brief periods of time (roughly on the scale of hours [~2] for several days [~5] in a row) during the deployment period (6 wk) when maximum natural levels were likely to have been exceeded in some of the high nutrient treatment pools. However, the short duration and the relatively small degree to which they were exceeded leads me to conclude that the treatments generally spanned an ecologically relevant range during the deployment period, at least with respect to maximum concentrations.

Maximum nutrient levels is only one way of evaluating realism in nutrient treatments. Other considerations include flux, duration, and frequency of enrichment events, as well as the ratio of nutrient delivered. Nutrient ratios are known to be important to the structure and dynamics of phytoplankton assemblages, however relatively little is known about how nutrient ratios affect periphyton and macroalgal growth or assemblage structure (but see Atkinson and Smith 1983, Wheeler and Björnsater 1992, Hillebrand and Sommer 1999). This experiment did not address how nutrient ratios influenced algal growth patterns but the same ratio was supplied in each of the enrichment treatments. The manufacturers specifications indicated the formulation used contained a 1:1 ratio of N:P. Lab trials with dispensers demonstrated released ratios did not match the formulation, but did not differ between low and high dispensers (low, 6.11 ± 2.09 [mean ± 1 SD]; high, 6.89 ± 2.13; t test, $P = 0.23$), and were within the range of naturally occurring ratios for this region. Ambient nutrient ratios in Oregon fluctuate through time (Wheeler and Björnsater 1992); N:P taken monthly for 15 mo at Yaquina Head, Oregon ~18 km south of Boiler Bay ranged from 5 to 14 (mean ± 1 SD = 8 ± 2). Comparisons among treatments (ambient levels vs. enriched treatments) is difficult because continuous am-

bient nutrient measurements were not made. The issue is further complicated because macroalgae often uptake and store nutrients when ambient levels are high and use them for growth later when nutrients are limiting (Chapman and Lindley 1980, Wheeler and Björnsater 1992, Pedersen and Borum 1996, 1997). Additional research is needed to increase our understanding of the role that nutrient ratios play in regulating macroalgal assemblages.

Flux of nutrients to attached macroalgae is determined by concentration in the water column in conjunction with dynamics of flow and boundary layers around the algal frond and bottom topography. An alga fixed in space with a nutrient-rich medium constantly moving by it is in a very different environment than a single celled alga that moves with a mass of water. Flux rates from the dispensers were osmotically driven, thus when nutrient levels were high (naturally or due to the dispenser itself), release rates should have been reduced. Duration and frequency of high nutrient events is generally set by ecosystem-level fluxes such as upwelling events in eastern boundary current systems (or seasonal turnover in lake systems). Detailed resolution of the flow environment was not conducted and could not be evaluated beyond the relative differences among blocks and between the two sites. However, these sites are not atypical of protected to moderately exposed (i.e., not headlands) wave environments on gently sloping platforms along the Oregon coast (K. J. Nielsen, *personal observation*).

The duration of the nutrient treatment was for two six-week periods during low tides between May and August. Upwelling injects cold, nutrient rich water from depth into coastal areas raising overall nutrient levels. The frequency, intensity and duration of these events varies from year to year and with other large-scale phenomena such as El Niño. Typical upwelling events along the Oregon coast range from three to seven days (continuously) and occur between April and September (Huyer 1976). The timing of experimental nutrient enrichment was coincident with the times nutrients are often periodically high due to natural processes.

A limitation of the nutrient dispenser design used in this study is that it could not compensate for differential depletion rates (presumably during high tide) among sites with different flow regimes. It is therefore possible that differences in algal responses to the nutrient treatment between sites (e.g., exposure × nutrient effect for total algal biomass) may have been associated with differences in the nutrient treatment between sites rather than differences associated with wave exposure per se. However, other studies of how flow and waves effect nutrient delivery rates to (Larned and Atkinson 1997), and photosynthetic efficiency of (Wing and Patterson 1993), benthic macroalgae are consistent with the results and interpretation presented here. Additional study is needed to fully elucidate the relationship be-

tween benthic macrophyte abundance and productivity patterns, and the complex flow, nutrient and light fields of their environment.

Conclusions

This study has demonstrated that nutrients can be influential in determining the structure of algal assemblages in conjunction with refuges from herbivory even in an upwelling region where nutrients are rarely, if ever, considered a limiting factor for seaweeds (Leigh et al. 1987, Fujita et al. 1989, Wheeler and Björnsater 1992). However, the influence of nutrients on seaweeds was decoupled from herbivore abundance patterns. Large herbivores did not increase in abundance in response to nutrient additions, although some evidence suggested that smaller herbivores did increase in abundance in response to nutrient additions. The combined effect of morphological defenses of seaweeds, and the foraging range of the one of the dominant consumers relative to the scale of the experiments, were likely factors that contributed to this decoupling of herbivore from resource dynamics. The effect of nutrients on seaweeds was more pronounced in wave-protected pools in a manner that was logically consistent with a predicted hydrodynamic mechanism. Herbivores had a strong overall impact on algal abundance that declined at the wave-exposed site in agreement with top-down predictions of food chain models and previous research in rocky intertidal systems. Contrary to model predictions, herbivores had a negative effect on algal productivity. Apparently algal species with the potential to respond to increased nutrients had no effective refuge from herbivory in these tide pools.

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APPENDIX

A table of regression equations used to calculate invertebrate biomass and a figure showing the relationships between algal percentage cover and three measures of biomass (wet, dry, and ash-free dry masses) are available in ESA's Electronic Data Archive: *Ecological Archives* M071-004.