Ecology, 74(3), 1993, pp. 904–918

EFFECTS OF NITROGEN AVAILABILITY AND HERBIVORY ON EELGRASS (ZOSTERA MARINA) AND EPIPHYTES[1]

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Abstract. Although the growth of eelgrass *(Zostera marina)* is controlled by resources as well as higher order interactions with epiphytes and their herbivores, these constraints rarely are considered together. The ability to utilize both water column and sediment nutrient sources in a complex habitat may provide eelgrass with a partial release from nutrient competition with epiphytes that have more efficient uptake kinetics and can reduce eelgrass growth, particularly in eutrophic habitats. We investigated the relative effects of dissolved inorganic nitrogen in the water column vs. the sediments, and herbivory by the common isopod *Idotea resecata,* on eelgrass growth and epiphyte biomass in an intertidal eelgrass bed in Padilla Bay, Washington. In the field, we fertilized the sediments and/or the water column with ammonium and measured eelgrass growth and epiphyte biomass. We also monitored epiphyte biomass and water column nutrient concentrations and censused isopod densities. Laboratory experiments focused on the effects of *I. resecata,* fertilization of the water column and sediments, and depletion of sediment nutrients on eelgrass growth and epiphyte biomass. Most simply, we hypothesized that epiphytes would respond positively to increased water column nutrients as eelgrass would to increased sediment nutrients, and that herbivory on epiphytes could mitigate deleterious effects of epiphytes on eelgrass.

We demonstrated that eelgrass growth is affected both by sediment nitrogen resources and the higher order effects of epiphytes and their control by *Idotea resecata.* During our field experiments, growth of eelgrass leaves tended to increase in response to sediment fertilization; this trend was significant in April 1988 but not in August 1987. At both times, leaf growth rates demonstrated a saturation-type response to sediment ammonium concentrations >100 μmol/L, providing further support for nitrogen limitation of eelgrass growth over much of the range in ambient concentrations (30–137 μmol/L) in the sediment porewaters. Together, sediment ammonium concentrations and epiphyte biomass explained a significant portion (71%) of the variance in eelgrass leaf growth in August 1987.

Consideration of sediment nitrogen, epiphytes, or herbivores alone is unlikely to yield a predictable understanding of the control of eelgrass primary productivity in nature, particularly given the complexity of the eelgrass habitat with respect to its dual nutrient sources. For example, epiphyte biomass was predicted by our laboratory experiments and other data to be nitrogen limited in Padilla Bay, yet it was not correlated with ambient nitrogen concentrations nor did it increase with fertilization of the water column. These results can be reconciled by considering herbivory by *Idotea resecata.* In the laboratory, the isopod reduced epiphyte biomass by one-third and in its absence, epiphyte biomass increased with increasing nitrogen concentrations in the water column and negatively affected eelgrass growth.

Key words: epiphytes; eutrophication; Idotea resecata; *mesoherbivores; nitrogen limitation;* Zostera marina.

INTRODUCTION

The sustained interest of ecologists in determining the relative importance of resources vs. higher order interactions in controlling natural populations and communities is expanding to include recognition of the significance of abiotic and biotic heterogeneity (see Matson and Hunter 1992). In aquatic systems, particularly marine, research has centered on the effects of resources vs. higher order interactions on trophic dynamics (see Menge 1992, Power 1992, Strong 1992, and references therein), yet interest extends to an understanding of these effects on other population, community, and ecosystem processes, e.g., control of primary productivity. Although perhaps not framed in the terminology of bottom-up vs. top-down control, some marine research has contributed to the growing understanding that higher order interactions can con-

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[1] Manuscript received 27 February 1992; revised 20 July 1992; accepted 21 July 1992.

trol primary productivity through modulation of resources (Meyer et al. 1983, Carpenter 1986, Bray et al. 1986, Williams and Carpenter 1988, 1990), a linkage that has not been incorporated explicitly into current theoretical thinking (but see Power 1992 for discussion), and this perspective has expanded the research arena on marine plant–animal interactions beyond community structure aspects and antiherbivore defense theory. In this broader interpretation of the relative importance of resources and species interactions, our study addresses a presumably competitive interaction between primary producers (eelgrass and its epiphytes) that is hypothetically mediated by resource heterogeneity (unequal access to nutrient sources) and herbivory.

Seagrasses (Spermatophyta) inhabit soft substrata, and the extensive meadows they form rank among the most productive coastal ecosystems (McRoy and McMillan 1977). Although considerable attention has been given to limitation of seagrass growth by primary factors of light, temperature, and nutrients (e.g., McRoy and McMillan 1977, Orth 1977, Harlin and Thorne-Miller 1981, Williams and McRoy 1982, Short 1983, Dennison and Alberte 1985, Dennison et al. 1987), seagrass growth is affected by a more complex array of factors, such as hydrology (Fonseca and Kenworthy 1987) and species interactions (Wetzel and Neckles 1986, Williams 1987), including grazing (Thayer et al. 1985, Williams 1988), that undoubtedly modify the effects of primary factors. Epiphytes are one higher order effect that impinges substantially upon seagrass growth; declines of seagrasses and other submerged aquatic vascular plants have been attributed to epiphyte overgrowth in response to eutrophication (Orth and Moore 1983, Cambridge and McComb 1984, Twilley et al. 1985). In turn, herbivory on epiphytes can shift the outcome of the epiphyte–seagrass interaction (Orth and Van Montfrans 1984, Hootsmans and Vermaat 1985, Howard and Short 1986, Wetzel and Neckles 1986).

The nature of interactions between seagrasses and their epiphytes is quite diverse (Harlin 1980, Orth and Van Montfrans 1984). After epiphytes (primarily diatoms and filamentous algae) colonize seagrass leaves, they modify the microenvironment of seagrass leaves through shading, intercepting water column nutrients, and increasing the diffusive boundary layer, thus reducing oxygen, carbon (Sand-Jensen 1977, Sand-Jensen et al. 1985), and presumably nutrient supply. Conversely, seagrasses can inhibit epiphyte growth through release of soluble compounds (Harrison and Chan 1980, Hamson and Durance 1985). The effects of epiphytes on seagrasses are not always deleterious, e.g., reduction of desiccation of their host (Penhale and Smith 1977, Richardson 1980), protection from ultraviolet radiation (Trocine et al. 1981), and provision of nitrogen through fixation (McRoy et al. 1973).

Although the abundance of seagrass epiphytes has been correlated positively with water column nitrogen concentrations (Borum and Wium-Andersen 1980, Borum 1985, Twilley et al. 1985, Tomasko and Lapointe 1991), the sediment nutrient source for the seagrasses has not been considered as a factor affecting the interactions with epiphytes. Both seagrasses and epiphytes utilize water column nutrients, but epiphytes preempt nutrients by virtue of their physical position in the water column and superior nutrient uptake kinetics [Thursby and Harlin 1982 (eelgrass), Carpenter and Capone 1983 (diatoms), Wallentinus 1984 (filamentous algae)]. Increases in sediment nutrients, which the epiphytes can access only minimally through the seagrasses (Harlin 1973, McRoy and Goering 1974), should increase eelgrass growth and potentially dilute epiphyte biomass through increased turnover of the leaf substratum (Borum 1985).

Assessment of the relative importance of resource ("bottom-up" constraints) vs. the higher order interactions ("top-down" constraints) of epiphytes and herbivores on seagrass growth is complicated by the complexity of a habitat divided into below- and aboveground portions. This complexity represents a critical distinction from habitats, such as the rocky intertidal, where species interactions are restricted to the aboveground. Although terrestrial plants similarly inhabit a divided, three-dimensional environment, they rarely exploit nutrients from the air, unlike aquatic angiosperms and rhizophytic marine algae that utilize both sediment and water column nutrients (McRoy and Barsdate 1970, McRoy and Goering 1974, Williams 1984). To address the nature of species interactions in soft substrata, this habitat complexity must be considered. To this end, we present results of a study to determine: (1) the relative effects of nitrogen (ammonium) enrichment of the sediment vs. water column on epiphyte biomass and the growth of the seagrass *Zostera marina* (eelgrass); and (2) the importance of herbivorous isopods in controlling the seagrass-epiphyte interaction. In the past, the effects of sediment nutrients on eelgrass growth, of water column nutrient availability on epiphyte growth, and of herbivory on the eelgrass–epiphyte interaction have been investigated independently. We questioned whether ecological complexity, in the form of unequal access to multiple nutrient sources and species interactions at the primary and secondary trophic level, was important; would results be different if the combined effects were considered? Our results suggest that their combined effects on eelgrass growth indeed may lead to different outcomes.

METHODS

Study site

Our study site was in the intertidal portion of Padilla Bay National Estuarine Research Reserve (PBNERR) in north Puget Sound, Washington, USA. The eelgrass bed within the reserve is one of the largest continuous seagrass habitats (2854 ha, Webber et al. 1987) on the west coast of North America. It provides an important habitat for juvenile Pacific salmon that prey on epibenthic crustaceans associated with eelgrass epiphytes (Simenstad et al. 1982, 1988) and a stopover and overwintering site for migratory Black Brant Geese. Two eelgrass species comprise the beds in PBNERR, the native Zostera marina and Zostera japonica, introduced to the eastern Pacific with oyster culture in the 1920s. Eelgrass and epiphytes contribute equally to net primary production in this estuary (Thom 1990). PBNERR is pristine, although it is surrounded by farmlands and is across the bay from a major oil refinery.

In situ ammonium enrichment experiments

Two in situ ammonium enrichment experiments were performed (7–23 August 1987, 17 April–5 May 1988) after preliminary experiments in June and July 1987 to establish the fertilization protocol. A permanent sampling grid 30 x 30 m was established in an area of maximum density of Zostera marina (–0.3 m tidal elevation relative to mean lower low water [MLLW]), where Zostera japonica was rare. Low tides occurred during the day from March through September, when eelgrass was exposed to direct sunlight for 6–7 h. During the experiments described below, the sky was cloudy during only 4 d of the 1988 experiment. At high tide, the study site was covered by a maximum of 3 m water and on sunny days in spring and summer, the photon flux density reaching the bottom of the eelgrass (hereafter referring to *Z.* marina only) leaf canopy was >150 $\mu mol \cdot m^{-2} \cdot s^{-1}$, measured with a Biospherical underwater spherical quantum sensor and meter (model QSI-140, Biospherical Instruments, San Diego, California, USA). At this irradiance, light was unlikely to limit eelgrass growth during the experiments (Dennison and Alberte 1985). Salinity was 28 g/kg.

Treatments consisted of adding ammonium chloride to the water column (W), sediment (S), or water column plus sediment (WS) in randomly chosen, replicated plots ($n = 7$) marked at the sediment surface by 25 × 25 cm wire quadrats anchored in the sediment. Similarly replicated control plots (C) received no added ammonium. An area of 1 m^2 surrounding the plots was not resampled during subsequent experiments. Fertilized plots were ≥3 m apart, and controls were located >4 m from fertilized plots. Pathways across the study site were maintained to minimize disturbance.

Fertilizer nitrogen was delivered as ammonium chloride, with 10 g held in a nylon mesh bag inside a capped 50-mL plastic centrifuge tube with holes drilled in the sides. The water column was fertilized with two tubes placed inside a plastic "spill" cup (to contain concentrated ammonium dripping out at low tide) attached to a steel reinforcing rod inserted in the center of the quadrats within the leaf canopy. Sediments were fertilized by placing one similar tube in the sediments in the center of a plot. Ammonium-free tubes likewise were placed as disturbance controls in the sediments and/or water column in all plots.

Although there is considerable speculation concerning the relative importance of nitrogen vs. phosphorus in limiting seagrass growth (Short 1987, Duarte 1990), nitrogen is more likely to be limiting in the clastic sediments (Berner 1980) of Padilla Bay. Nitrogen limitation of eelgrass has been reported (Harlin and Thorne-Miller 1981, Short 1983; W. Dennison, personal communication) and has been hypothesized for eelgrass and algae in Puget Sound (Thom and Albright 1990). We fertilized with ammonium because it is the dominant inorganic nitrogen species in anoxic sediments typical of seagrass beds and because fertilizers used in agriculture adjacent to the bay are ammonium based. The sediment enrichments provided double the mass of nitrogen per unit area of sediment in a previous in situ fertilization (phosphorus also supplemented) of an eelgrass bed (Orth 1977). Harlin and Thorne-Miller (1981) conducted the only recent in situ fertilization of the water column over eelgrass beds. Our water column treatment (6.7 g/0.0625 m^2 over 15 d in August and 5 g/0.0625 m^2 over 12 d in April) was on the order of the ammonium supplement of this earlier experiment (86–271 $g \cdot m^{-2} \cdot d^{-1}$). Our experiments were the first to test for single-nutrient limitation of eelgrass growth under field conditions without disrupting the clonal architecture of eelgrass.

In 1987, we fertilized plots on 7 August and water column tubes were replaced as frequently as logistics allowed (8, 9, 13, and 17 August). Every eelgrass shoot within each plot was marked for growth by pushing a syringe needle through the shoot in the region of the nongrowing leaf sheath. Eelgrass was marked on 8 August and harvested on 22 August. In 1988, we fertilized plots on 17 April and replaced water column tubes on 19, 24, and 29 April. Eelgrass was marked on 18 April and harvested 3 May.

At harvest, all eelgrass shoots were collected from the plots and 10 and 12 randomly selected shoots were processed for epiphytes and growth measurements in August 1987 and May 1988, respectively. Epiphytes on all the leaves within a shoot were scraped into a small amount of freshwater, filtered onto preweighed filter papers, dried at 90°C, and weighed. We observed no calcareous epiphytes on eelgrass leaves and, for logistical simplicity and ease of comparison with past studies, chose not to ash samples. Although meiofauna such as nematodes and copepods were undoubtedly included, large individuals (snails, isopods, amphipods) were removed before drying. Shoots were separated into new vs. old growth from the reference hole in the nongrowing sheath and the length of the new growth of all leaves was measured. We also sampled epiphyte biomass ($n = 15$ shoots) periodically in the vicinity of the study site from June 1987 through Au-

TABLE 1. Design of the laboratory diffuser experiment: number of diffusers in manipulations of ammonium availability in the water column and sediments.

Water column manipulations	Sediment manipulations*			
	Depleted†	Ambient‡	5 mmol/L§	20 mmol/L§
	Number of diffusers			
Ambient (1 μmol/L)	2	2	–	–
Ambient (1 μmol/L)	–	–	2	2
Enriched (10 μmol/L)‖	2	2	2	2
Enriched (33 μmol/L)‖	2	2	2	2

* Refer to ***Results*** for porewater concentrations achieved in the sediment treatments. Concentrations of (nitrate + nitrite) in the water column ranged from 20 to 30 μmol/L in each aquarium. Dashes reflect that fertilized sediment treatments were separated from unfertilized ones to avoid enrichment of the unfertilized water column.

† N-free seawater maintained in porewater reservoir.

‡ 100 μmol/L (average concentration in porewaters of eelgrass bed in Padilla Bay) in porewater reservoir.

§ Concentration maintained in porewater reservoir.

‖ Concentration maintained in water column.

gust 1989 and made qualitative examinations of the epiphyte load during late fall and winter of each year.

Water samples for ammonium and (nitrate + nitrite) concentrations were taken from three randomly selected plots in each treatment primarily at low tide in receding, flooding, or standing water of ≈15–60 cm depth. Water was collected within the canopy and occasionally from spill cups prior to and after fertilizer replacement and filtered immediately through 0.2 μm mesh glass-fiber filters using a syringe filter holder. All sampling gear was acid-cleaned prior to usage. Samples were shaded until transported to shore (<3 h later) where ammonium reagents were added and (nitrate + nitrite) samples were frozen for subsequent analysis (Koroleff 1976, Parsons et al. 1984). Triplicate samples were taken in the vicinity of the study site at other times during 1987-1988. Temperatures in the water column and upper 3 cm of sediments were measured at each sampling time.

Sediments for porewater ammonium analyses were collected at the end of each experiment using corers made from 50-mL syringes with cut-off ends. In each of three randomly selected plots per treatment, one core was taken in the center of the plot next to the fertilizer tube and a second at the farthest edge of the plot. Cores were transported in a cooler with ice packs to the laboratory for processing up to 6 h later. Cores were sectioned in 5-cm increments to 15 cm and centrifuged to extract porewaters. Concentrations from the 2 cores/plot were averaged and will be reported only for the 0–5 cm sections, where the majority of eelgrass roots occur; deeper sections typically had slightly higher concentrations. A preliminary analysis indicated that degassing porewater with N_2 gas after appropriate pH adjustment to remove H_2S interference did not yield higher ammonium concentrations than did diluting porewaters with reagent-grade deionized water to keep analyses within the limits of Beer's Law.

Kinetic analysis of eelgrass growth

If eelgrass growth was nitrogen limited, the growth rate would be expected to show a saturation-type response to sediment ammonium concentrations where growth is a linear function of concentration (i.e., ammonium is limiting) up to a critical concentration above which no further enhancement of growth occurs (growth is "saturated"; ammonium is not limiting). Saturation-type responses can be described by the Michaelis-Menten function (Williams and Fisher 1985). Regression coefficients from a Woolf linear transformation (concentration/growth rate vs. concentration) of the Michaelis-Menten function (Dowd and Riggs 1965) were used to assess the fit of the data to the function and to derive the following constants: (1) the concentration at which one-half the maximum growth rate is achieved, called the half-saturation constant (K), and (2) the maximum growth rate. These constants were substituted into the hyperbolic-tangent form of the function to provide a smooth plot of the function for comparison to actual data points.

Sediment diffuser experiment

Because variability in fertilizer release is difficult to control in the field, we initiated a laboratory manipulation of sediment porewater and water column ammonium concentrations in December 1987 (Table 1). This experiment enabled us to achieve higher concentrations of ammonium in the water column than was possible in the field and permitted depletion as well as enrichment of sediment nitrogen concentrations. Twenty-four cores of *Zostera marina* intact with sediments from Padilla Bay were acclimated for over a month in plastic flower pots in aquaria with running ambient seawater and then placed in sediment diffusers (opaque polycarbonate containers divided into a central area to hold an eelgrass sediment core and an outer ring holding a porewater reservoir, connected by small, mesh-covered holes) identical to those of Dennison et al. (1987). The porewater reservoirs of the diffusers were in contact with the sediment–eelgrass core, which allowed manipulation of sediment porewaters by establishing a diffusional concentration gradient. Diffusers disrupted the clonal architecture of eelgrass. If physiological integration within an eelgrass clone is important for metabolism and growth, as found for another seagrass species (Tomasko and Dawes 1989), this disruption may result in low growth rates.

Diffusers were assigned randomly to four 75-L aquaria with ambient seawater delivered at 3.2 L/min, two with ambient seawater ammonium concentrations (1 μmol/L, see below, *Sediment diffusion experiment*, for rationale), one enriched to 10 μmol/L, and one enriched to 33 μmol/L ammonium. These enrichments were within the seasonal range of concentrations in waters entering Padilla Bay (Wissmar 1986) and at other sites in Puget Sound (Thom and Albright 1990). Relatively constant levels of water column enrichment were established by regulating the delivery rate of a concentrated ammonium chloride stock solution into the aquaria. Ammonium and (nitrate + nitrite) concentrations in the water in each aquarium were measured in duplicate every 1–3 d.

Within each water column treatment, duplicate diffusers were maintained at ambient, depleted, and two levels of enriched ammonium concentrations in the eelgrass sediments by establishing an ammonium concentration gradient between the seawater in the reservoir and the sediment porewater (Table 1). "Ambient" sediment concentrations were maintained by filling the porewater reservoirs with seawater of the average ammonium concentration (100 μmol/L) measured in porewaters at the study site; thus, little concentration gradient should have existed between the reservoir and the sediments in the core. In the "depleted" sediment treatment, ammonium-free seawater was maintained in the reservoir. In addition, ammonium enrichments were achieved with porewater reservoirs maintained at 5 and 20 μmol/L. The solutions in the porewater reservoirs were replaced with fresh solutions of the appropriate concentrations every **3** d. The four enriched sediment diffusers of the ambient water column treatment were placed in a separate aquarium from the two ambient and two depleted sediment diffusers to reduce contamination of the ambient water column with ammonium from sediments, which amounted to 0.23 μmol/L above ambient. Light was maintained at 250–310 pmol of photons$\cdot m^{-2} \cdot s^{-1}$ at the leaf canopy for 13 h/d (growth-saturating conditions, Dennison and Alberte 1985), and water temperatures were measured daily. All eelgrass shoots ($n = 26–62$) in each diffuser were marked for growth measurements 17 d after establishment of ammonium treatments. Growth and epiphyte biomass of 6 shoots/diffuser were measured 10 d later and averaged. Porewater ammonium concentrations were obtained in duplicate from 0 to 5 cm sediment depth in each diffuser using syringe corers. Isopod and mollusc grazers were not present, but small crustacean grazers such as caprellid amphipods were not controlled and their effect was assumed similar in each aquarium.

Isopod herbivory experiment

We counted all Idotea resecata in the marked (25 x 25 cm) plots of the fertilization experiment or 25 x 25 cm quadrats placed temporarily in the eelgrass during low tide. With practice, we recognized isopods immigrating to or emigrating from the quadrats as we separated the leaf canopy and adjusted counts accordingly. Although this is a crude method for censusing mobile fauna, it allowed estimation of relative abundances.

Based on field and preliminary laboratory observations (see Results: Herbivory on epiphytes), we conducted a laboratory experiment to discern the effect of herbivory by Idotea resecata on epiphyte biomass and growth of Zostera marina. In early August 1987, I. resecata were collected in the field and transported in coolers to the laboratory where they were measured and held in aquaria with running seawater and a source of eelgrass and epiphytes. Eelgrass and sediments were collected nearby the permanent sampling grid in Padilla Bay using corers (15 cm diameter) and transferred intact to plastic flower pots. Eelgrass shoots were counted (18 ± **3** shoots/core [mean + 1 s ~]) and marked for growth measurements as described previously. I. resecata and epiphytes were removed carefully before four pots were placed in each of two aquaria with running seawater. I. resecata 20–30 mm long were added to one aquarium at natural densities (1 isopod/7 leaf shoots). No I. resecata were added to the other (control) aquarium. Isopods were counted every few days and restocked if necessary. We did not control other mesoherbivores such as littorines, amphipods, and copepods and assumed their effect was equal between treatments. Our preliminary observations indicated these herbivores had a minor effect on epiphyte biomass relative to I. resecata (see Results: Herbivory on epiphytes). Growth-saturating light conditions for eelgrass were maintained. Water temperatures were measured daily and water was sampled for ammonium and (nitrate + nitrite) every few days. Leaf growth of all shoots over a 17-d period was measured nondestructively in August, and pots were returned to the aquaria after measurements. All shoots were remarked a few days later; of these, 6 shoots/pot were measured for growth and epiphyte biomass after 20 d. Mean values per pot were averaged over all pots in each aquarium. Mean results were not compared statistically between treatments because aquaria were not replicated within a treatment.

Statistical analyses

Our question in the field nitrogen fertilization experiments was whether sediment fertilization resulted in significantly different eelgrass growth or epiphyte biomass than water column fertilization or no fertilization treatments. Fertilization treatment effects were partitioned into + or – water and + or – sediment and analyzed in a two-way ANOVA using Type I sum of squares. Statistical Analysis Systems programs (SAS 1981) were used. We did not fix the experimentwise error rate (Rice 1989) of our ANOVAs, based on alternative arguments (Carmer and Walker 1982, Mead 1988, Hurlbert 1990) and the precedent of Soto and Hurlbert (1991). Statistical power (the probability of rejecting a false null hypothesis of no significant difference) was calculated using $a = .05$, with an effect size of f, the standard deviation of the ANOVA cell means divided by the common standard deviation of all cells (Cohen 1988).

TABLE 2. Dissolved ammonium concentrations in the water column in experimental field treatments, including preliminary experiment in July 1987. $n = 3$ treatment replicates. Time is relative to replacement of fertilizer.

			Locus of NH_4Cl addition			
Date	Time	Control	Water	Sediment	Water + sediment	Spill cups
		Dissolved ammonium (μmol/L, mean ± 1 SD)				
7 Jul 87	−1 h	0.22 ± 0.16	0.06 ± 0.10	0 ± 0	0.82 ± 1.28	
8 Jul87	+24 h	0.37 ± 0.15	0.56 ± 0.02	0.33 ± 0.03	0.78 ± 0.68	···
9 Jul 87	+24 h	0.51 ± 0.29	0.85 ± 0.60	0.47 ± 0.46	0.79 ± 0.55	···
10 Jul87	+2 h	6.4 ± 7.7	13 ± 14	0.93 ± 0.47	47 ± 79	···
Grand mean		1.9 ± 3.0	3.6 ± 6.3	0.43 ± 0.39	12 ± 23	···
8 Aug 87	+26 h	0.50 ± 0.55	1.3 ± 1.8	0.32 ± 0.13	0.69 ± 0.57	···
9 Aug 87	+24 h	3.0 ± 3.0	1.9 ± 1.2	4.2 ± 2.4	3.0 ± 2.8	143 ± 1.07
	+.5 h	2.9 ± 2.1	94 ± 124	3.4 ± 1.6	178 ± 65	···
13 Aug 87	+4 d	4.2 ± 3.9	3.8 ± 1.8	1.2 ± 0.63	5.8 ± 4.9	···
17 Aug 87	+6 d	1.8 ± 0.16	1.8 ± 0.05	2.0 ± 0.06	2.0 ± 0.34	
Grand mean		2.5 ± 1.4	21 ± 41	2.2 ± 1.6	38 ± 78	···
19 Apr 88	+2 d	1.5 ± 0.37	34 ± 50	1.2 ± 0.41	4.1 ± 1.9	···
24 Apr 88	+5 d	0.49 ± 0.11	0.56 ± 0.06	1.7 ± 1.7	0.40 ± 0.06	···
	+.5 h	···	184 ± 16	···	63	···
29 Apr 88	+5 d	1.7 ± 0.61	0.93	3.1 ± 2.5	1.7 ± 0.36	···
5 May 88	+6 d	1.5 ± 0.31	3.1	2.0 ± 0.27	2.0 ± 0.13	114 ± 61
Grand mean		1.3 ± 0.53	45 ± 79	2.0 ± 0.80	14 ± 27	

To distinguish the relative importance of epiphyte biomass vs. sediment ammonium for eelgrass growth, standard partial regression coefficients were computed using a linear model (SYSTAT 1985). Mean growth per plot or diffuser was regressed against sediment ammonium and mean epiphyte biomass. The sample size for the regressions was smaller than for ANOVAs because some plots were not sampled for nutrients.

RESULTS

Despite tidal exposures of 6–7 h through midday, eelgrass exhibited no signs of physiological stress. Most leaves were releasing gas as is typical for actively photosynthesizing seagrass. In August, the leaf canopy dammed receding waters and the leaves were never completely exposed (lowest tides = −1.04 m MLLW). During the summer, the water column at low tide warmed to a maximum of 5°C above the temperature at the sediment surface, which ranged seasonally from 8.5" to 20°C. During the fertilization experiments, sediment temperatures were optimal for eelgrass growth (16"–17°C in August and 10"–18°C in April; Setchell 1929, Phillips 1984).

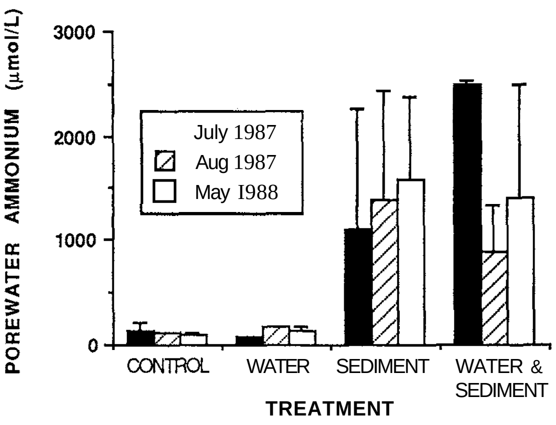

FIG. 1. Ammonium availability in porewaters in upper 0–5 cm of sediment during in situ fertilization experiments. Means and 1 SD, $n = 3$ treatment replicates, mean of two cores per replicate.

In situ ammonium enrichment experiments

Because nutrient delivery in in situ fertilizations of the water column is intrinsically pulsed, particularly in dynamic estuaries such as Padilla Bay, nutrient concentrations during the experiments were highly variable (Table 2). One hour after ammonium application, water column concentrations reached a maximum of 195 μmol/L. Sixty-four percent of the mean ammonium concentrations of the W and WS plots were higher than the control values when sampled from 0.5 h to 6 d postfertilization; time-averaged concentrations were higher by 26–36 μmol/L in the W and WS treatments. Low concentrations, however, did not indicate ineffective fertilization; high ammonium concentrations in water collected in the spill cups during tidal exposure at the end of the longest time between replacements (6 d) indicated that nitrogen still was being delivered to the plots. Concentration differences between treatments represent minima because most samples were taken during periods of rapid tidal exchange in Padilla Bay and because the concentrations are the equilibrium between fertilizer dissolution rates, dilution by diffusion and advection, and plant and algal uptake rates. Assuming all fertilizer dissolved, 100 and 80 g of nitrogen per plot were delivered to the water

TABLE 3. Epiphyte dry biomass of *Zostera marina* during in situ ammonium enrichment of water and/or sediments, and ANOVA results.

		Epiphyte biomass (mg/shoot, mean ± 1 SD)			
Treatment		8–22 August 1987		18 April-3 May 1988	
Control		14.0 ± 4.2		21.9 ± 3.6	
Water		10.0 ± 1.6		20.7 ± 7.9	
Sediment		12.3 ± 3.3		18.2 ± 5.5	
Water + sediment		10.2 ± 3.4		15.7 ± 4.2	
ANOVA results	df	F	P	F	P
Overall	3,24	2.27	.11	1.75	.18
Water	1, 24	5.82	.02	0.78	.39
Sediment	1, 24	0.38	.54	4.39	.05
Water x sediment	1, 24	0.61	.44	0.09	.77

column during the course of the August 1987 and April 1988 experiments, respectively.

Sediment ammonium concentrations also were increased by fertilization (Fig. 1). The concentrations at the end of the experiments represented the residual of ambient porewater ammonium plus dissolved fertilizer minus diffusive losses to the water column minus plant uptake. Average concentrations (≈1000–2000 μmol/L) in fertilized treatments were at least an order of magnitude higher than in controls (30–137 μmol/L). Ammonium concentrations decreased by typically 500 μmol/L from the center to the edge of the fertilized plots (≈10 cm distance).

Contrary to predictions, epiphyte biomass was not highest in treatments where the water column was fertilized (Table 3). In August, the effect of water column fertilization was opposite to predictions; epiphyte biomass was reduced significantly ($P < .02$) in these treatments. In April, there was again a lack of expected correspondence between epiphyte biomass and water column ammonium concentrations.

Eelgrass leaves tended to grow slowest in the unfertilized control plots and fastest when the sediments were fertilized (S plots in August 1987; WS in April 1988; Table 4). The effect of sediment fertilization was significant in April ($P < .003$). This was the fastest response (15 d) of eelgrass growth to nutrient availability that has been reported (Orth 1977, Harlin and Thome-Miller 1981, Dennison et al. 1987). Although the sediment fertilization effect was not significant in August, the power (the probability of rejecting the null hypothesis of no effect, Cohen 1988) of the ANOVA was low (0.44).

A Michaelis–Menten analysis of eelgrass growth vs. sediment ammonium concentrations further supports the hypothesis that sediment ammonium concentrations can limit eelgrass growth. In April, eelgrass growth showed a classical saturation-type response to sediment ammonium concentrations (Fig. 2); the regression coefficient of the Woolf plot was very high (0.98) and the half-saturation constant *(K)* was 96 μmol/L, a value virtually identical to one predicted from four other eelgrass studies (Dennison et al. 1987). Eelgrass leaf growth in the August experiment also showed a saturation-type response to sediment ammonium concentrations (regression coefficient of the Woolf plot =

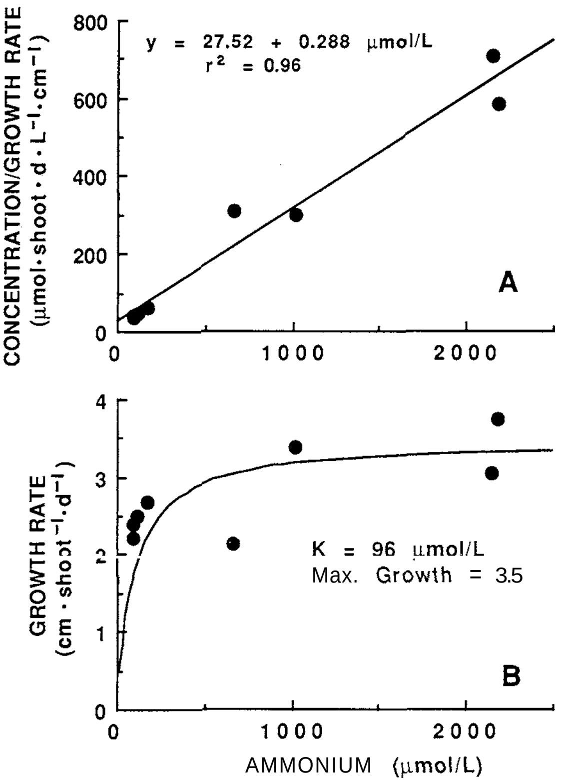

FIG. 2. Kinetic analysis of eelgrass leaf elongation in April 1988 as a function of ammonium concentration in sediment porewaters. Panel A is a Woolf linear transformation (Dowd and Riggs 1965) used to derive the kinetic constants of the Michaelis–Menten function shown in panel B. K = half-saturation constant.

TABLE 4. Growth (n = 7 shoots) of *Zostera marina* during in situ fertilization of water column and/or sediments and ANOVA results.

		Leaf growth (cm.shoot^{1}·d^{-1}, mean ± 1 SD)			
Treatment		8–22 August 1987		18 April-3 May 1988	
Control		3.16 ± 0.34		2.68 ± 0.29	
Water		3.28 ± 0.20		2.72 ± 0.46	
Sediment		3.62 ± 0.35		3.17 ± 0.35	
Water + sediment		3.47 ± 0.78		3.33 ± 0.62	
ANOVA results	df	F	P	F	*P*
Overall	3,24	1.34	.29	3.75	.02
Water	1, 24	0.01	.93	0.37	.55
Sediment	1, 24	3.41	.08	10.76	.003
Water x sediment	1, 24	0.60	.45	0.12	.73

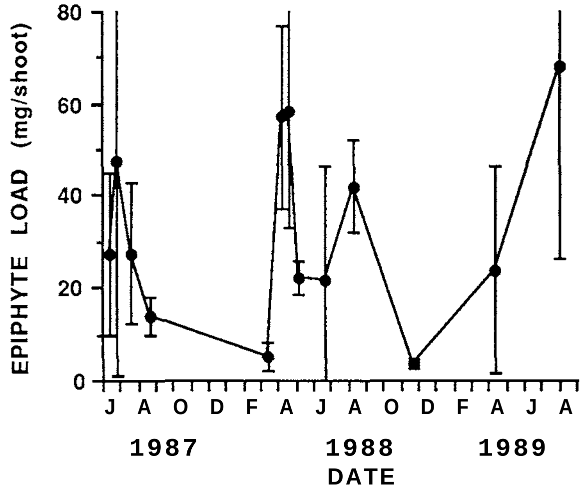

FIG. 3. Seasonal epiphyte dry biomass on *Zostera marina* in the vicinity of the study site. Means ± 1 so, $n = 15$ shoots.

0.97) and the predicted maximum growth rate was the same as the April experiment (3.5 cm·shoot^{-1}·d^{-1}), with K equal to 69 μmol/L. Thus, over much of the range in the mean ambient porewater concentrations of ammonium (30–137 μmol/L) measured in the upper 10 cm of sediment, the potential for nitrogen limitation of eelgrass growth existed in August and April.

Epiphyte biomass

From June 1987 through April 1989, epiphyte biomass of Zostera marina varied by up to an order of magnitude (Fig. 3), with minima occurring in fall and winter, based on quantitative and qualitative observations in the vicinity of the study area. The temporal changes in mean epiphyte biomass were similar to those reported elsewhere in Puget Sound eelgrass beds (Thom 1990). Epiphyte biomass was maximally 75% of eelgrass leaf biomass but more typically <20% (S. L. Williams, unpublished data).

Diatoms comprised virtually all of the epiphyte biomass. *Isthmia nervosa,* forming branched chains of cells 1 mm wide, was particularly abundant in spring 1987. *Enteromorpha* spp. and Myrionema sp. were collected occasionally.

The prediction that epiphyte biomass was limited by nitrogen concentrations in the water column was not supported. Under nitrogen limitation, epiphyte biomass should have paralleled the direction and magnitude of seasonal changes in dissolved nitrogen, given typical doubling times of 3–6 d for eelgrass epiphyte biomass (Borum 1987). Instead, although combined ammonium and (nitrate + nitrite) concentrations were always low (<3 μmol/L; Fig. 4) compared to other habitats in Padilla Bay and elsewhere in Puget Sound (Wissmar 1986, Thom and Albright 1990), they were highest from late fall through winter (until March) during the time when epiphyte biomass was lowest (Fig. 3; S. L. Williams and M. H. Ruckelshaus, personal observation). The correlation between epiphyte biomass and nutrients was poor ($r = 0.38$, $n = 8$ sampling dates for which epiphyte and ammonium plus [nitrate + nitrite] data were available). Furthermore, the magnitude of the changes in nutrient concentrations was small compared to changes in epiphyte biomass (Figs. 3 and 4; there are no nutrient data from 1989). These observations support the results of the in situ fertilization experiments that nitrogen in the water column was not a major factor controlling epiphyte biomass in Padilla Bay. Results from laboratory experiments (see below, *Diffuser* experiment), however, indicated that epiphyte biomass accumulation was nitrogen limited.

Herbivory on epiphytes

Herbivory may have had a stronger effect on epiphyte biomass than nitrogen availability, particularly in summer. The reduction of epiphyte biomass by half from July to August 1987 was correlated with a large increase in size and number of actively grazing Idotea resecata. I. *resecata* densities were 115 ± 82 individuals/m^2 (mean ± 1 SD, $n = 28$ plots) in early August 1987, 11 ± 17 inds./m^2 ($n = 24$) in May 1988, and 78 ± 26 inds./m^2 ($n = 4$) in August 1988. Carapace lengths were 2.5 ± 0.5 cm ($n = 232$ individuals), 1.0 ± 0.2 cm ($n = 12$), and 1.9 ± 0.5 cm ($n = 19$) in August 1987 and March and August 1988, respectively. We observed fewer and smaller I. resecata during fall and winter through January 1989, a pattern subsequently quantified (R. M. Thom et al., unpublished data).

Idotea resecata had a much greater effect on epiphyte biomass than other herbivores, as observed previously (Hootsmans and Vermaat 1985). Although other mesoherbivores such as caprellid and gammarid amphipods, the molluscs Lacuna spp., Phyllaplysia taylori, *Haminoea* spp., and rarely Idotea *wosnesenskii* were also present on eelgrass leaves at the study site, our impression that I. resecata was the most numerous mesoherbivore was later verified quantitatively (R. M. Thom, unpublished data). Caprellids were qualitatively

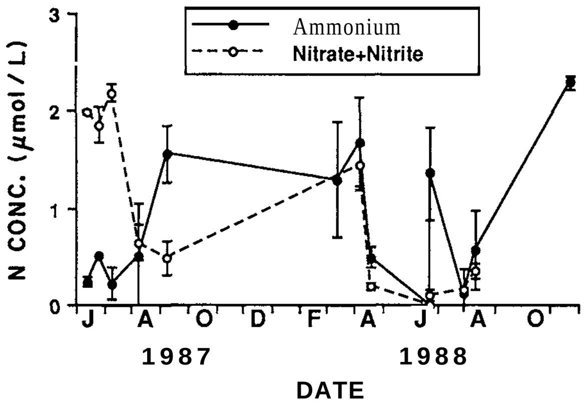

FIG. 4. Inorganic nitrogen concentrations in the water column in the vicinity of the study site. Means ± 1 so, $n = 2$–3 plots.

TABLE 5. Effects of grazing by the isopod *Zdotea resecata* on *Zostera marina* growth and epiphyte biomass. Means ± 1 SD.

	+ *Zdotea*	– *Zdotea*
Z. marina growth* (cm·shoot^{-1}·d^{-1})		
10-22 Aug 1987	1.6 ± 0.3	1.2 ± 0.2
2–22 Sep 1987	1.3 ± 0.6	1.2 ± 0.2
Epiphyte dry biomass? (mg/shoot)		
22 Sep 1987	7.8 ± 2.4	23.6 ± 7.4

* $n = 4$ cores; 12–22 shoots averaged/core.
† $n = 4$ cores; 6 shoots averaged/core.

less abundant in the summer than in winter and spring. In aquaria devoted to other eelgrass experiments, caprellid and gammarid amphipods were numerous (predators were absent) as were snails that reproduced in the aquaria (*Lacuna* spp., *Phyllaplysia, Haminoea*) and yet we needed to remove the luxuriant epiphyte loads to maintain eelgrass vigor. Epiphytes in these aquaria were reduced visibly only when *I. resecata* were added.

At natural densities (1 isopod/7 shoots), *Idotea resecata* reduced epiphyte biomass to one-third the value in the aquarium without *I. resecata* (Table 5). Eelgrass tended to grow faster under isopod grazing, although the growth rates were lower than in the field (Table 5), despite optimal temperature (14°–19°C; Setchell 1929, Marsh et al. 1986, Bulthuis 1987) and light conditions in the aquaria. Also, *I. resecata* exerted control over epiphyte biomass despite the relatively high concentrations of dissolved ammonium plus (nitrate + nitrite) (15.6 ± 0.4 μmol/L, $n = 5$ sampling dates) that should have fostered epiphyte blooms in both aquaria (see *Diffuser experiment* below). At artificially high densities in a reserve aquarium, *I. resecata* ate eelgrass shoots after removing all epiphytes; however, we saw little evidence of direct grazing on eelgrass leaves in the field.

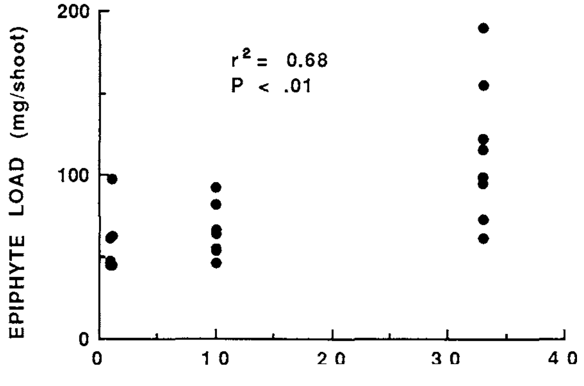

FIG. 5. Epiphyte biomass vs. ammonium availability in the water column in the diffuser experiment. Points are means of six shoots per diffuser. (Nitrate + nitrite) concentrations were 20-30 μmol/L at each ammonium level.

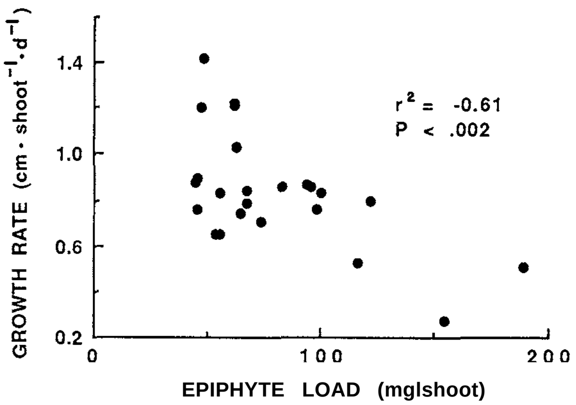

FIG. 6. Leaf growth of *Zostera marina* vs. mean epiphyte biomass in the diffuser experiment. Points are means of six shoots per diffuser.

Diffuser experiment

In this experiment, epiphyte biomass responded as predicted to eutrophication of the water column; epiphyte biomass was significantly and positively related to ammonium concentrations in the water column (Fig. 5). Ammonium concentrations in the water column were maintained at 0.87 ± 0.96 and 1.1 ± 6.9 μmol/L ($n = 8$ sampling dates, approximately every 3rd d during the experiment) in the two ambient aquaria and 10 ± 6.5 and 33 ± 29 μmol/L in the water column fertilizations; (nitrate + nitrite) concentrations were similar among aquaria and ranged from 20 to 30 μmol/L during the experiment. The maximum combined concentrations of dissolved inorganic nitrogen (66 μmol/L) in this experiment are within the seasonal range of concentrations in Puget Sound, including other sites in Padilla Bay (Wissmar 1986, Thom and Albright 1990). Epiphyte biomass in this experiment was at least double the biomass measured in the other experiments of the study and, at the highest level of ammonium enrichment, epiphyte biomass was also higher than the peak biomass in the field.

Eelgrass leaf growth declined significantly with increasing epiphyte biomass (Fig. 6). Eelgrass growth was not correlated with sediment ammonium concentrations (Fig. 7) despite the effective reduction or increase in the ammonium concentrations (5–1056 μmol/L) relative to control values (100 μmol/L). The maximum eelgrass growth rate was half the mean value in the field experiments, despite optimal irradiances and daily light periods.

Conditions for this experiment differed from those in the field in ways that should have favored epiphytes but not eelgrass, and this may explain why the response of epiphytes and eelgrass to nitrogen availability also differed from the field results. For one, no *Idotea resecata* were present. Second, concentrations of combined inorganic nitrogen in the water column were minimally an order of magnitude higher than at the study site in Padilla Bay (Fig. 4) because (nitrate +

TABLE 6. Densities of *Zdotea resecata* (no. individuals/0.0625 m^2) in *Zostera marina* fertilization treatments. *n* = 5 plots for control and water on 8 Aug 1987 and *n* = 7 elsewhere.

Date	Control	Locus of NH_4Cl additions: Water	Sediment	Water + sediment
8 Aug 1987	6.7 ± 7.3	8.7 ± 6.2	7.1 ± 3.1	7.2 ± 5.1
3 May 1987	1.4 ± 0.6	0.3 ± 0.5	0.8 ± 0.2	0.6 ± 1.0

nitrite) was consistently higher in the seawater supply to Friday Harbor Laboratories. The experiment also was conducted during the winter when the mean water temperature in the aquaria was 10.1° ± 0.3°C, the thermal limit below which cold rigor occurs in eelgrass (Setchell 1929, Marsh et al. 1986, Bulthuis 1987). Slower growing eelgrass provides epiphytes an extended opportunity to colonize and grow before a leaf is sloughed (Borum 1987).

Relative effects of epiphytes vs. sediment ammonium on eelgrass growth

In both in situ fertilization experiments, eelgrass grew slowest in the control plots that also had the highest epiphyte biomass, and in April 1988, eelgrass grew fastest in the treatment with the lowest epiphyte biomass (water + sediment fertilization). High growth rates could have resulted from low epiphyte loads and/or increased nitrogen concentrations in the sediments. In the latter case, low epiphyte biomass could have resulted secondarily from increased turnover of the leaf substratum, but this is unlikely because the difference in new growth among treatments was <1 cm and the experiment was short enough to preclude most epiphyte colonization of new growth. We used multiple regression to analyze the relative effects of epiphyte biomass and sediment ammonium concentrations on the variance in eelgrass growth rates. First, however, we addressed the question of whether differences in epiphyte biomass resulted from differential isopod abundances among treatments, hypothetically in response to nitrogen-enriched epiphytes.

Numbers of *Idotea resecata* were not significantly different among treatments 3 d (August 1987) and 15 d (May 1988, end of experiment) into the experiment (one-way ANOVA; Table 6). We observed no qualitative differences in abundances of other herbivores among the plots. Also, amphipods can reduce eelgrass epiphytes (Caine 1980), but their abundance in Padilla Bay was correlated with heavily, not lightly, epiphytized eelgrass (Simenstad et al. 1988). These observations suggest that trends in epiphyte biomass among treatments were not the result of differential grazing.

TABLE 7. Multiple regression analysis of *Zostera marina* growth.

	August 1987 (*n* = 8)	April 1988 (*n* = 8)	Diffusers (*n* = 24)
Standard partial regression coefficients			
Epiphyte biomass	.340NS	−.005NS	−.602**
Porewater ammonium	.919*	.744*	−.133NS
Tolerance	.839	.997	.998
Correlation of regression coefficients	.401	,057	,045
r^2	.710*	.554NS	.388**

* P = .05; ** P = .01.

Standard partial regression coefficients indicate that eelgrass leaf growth was correlated more closely with sediment ammonium concentrations than epiphyte biomass in each field fertilization experiment (Table 7). The poor correlation of regression coefficients and high tolerance indicate that sediment ammonium and epiphyte biomass were independent, as expected. Together, these factors accounted for 55–71% of the variance in eelgrass growth. Standard partial regression coefficients also support the diffuser experiment result that epiphyte biomass was more important than sediment ammonium in explaining the variance in eelgrass growth under laboratory conditions (Table 7, Figs. 6–7).

DISCUSSION

A complex of factors including nitrogen availability, the interactions between epiphytes, eelgrass, and mesoherbivores, in addition to light and temperature, controls the growth of intertidal eelgrass in Padilla Bay. Our field experiments demonstrated that at least during

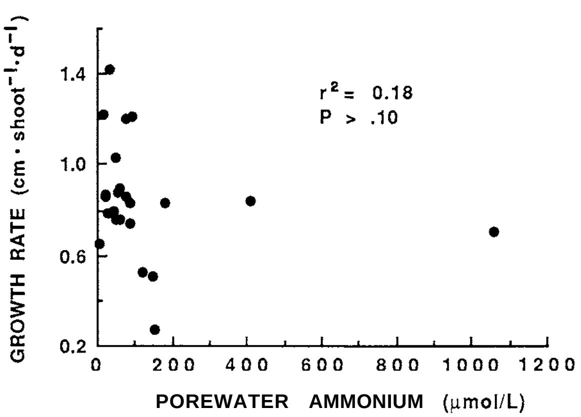

FIG. 7. Leaf growth of *Zostera marina* vs. ammonium concentration in sediment (0–5 cm depth) porewaters. Points are means of six shoots per diffuser.

the spring, when temperature and light are optimal for eelgrass growth, nitrogen availability in the sediments can limit intertidal eelgrass growth. This conclusion is supported by the significant effect of sediment fertilization on growth in April 1988 (Table 4), the saturation-type response of growth to ammonium concentrations in the sediment in August and April (Fig. 2), and the significant standard partial regression coefficients for porewater ammonium concentrations on growth rates (Table 7). The trend in mean growth rates across treatments in August 1987 (Table 4) also follows this conclusion, that the trend was nonsignificant was based on low statistical power. These experiments confirm the conclusion of Thom and Albright (1990), based on correlations between eelgrass standing stock and environmental parameters, that eelgrass in Puget Sound may be nitrogen starved. The kinetic analysis of eelgrass growth vs. ammonium concentrations in sediment porewaters (Fig. 4) also provides empirical support for the suggestion of Dennison et al. (1987) that concentrations <100 μmol/L should limit eelgrass growth. Thus, the control of eelgrass growth at our site in Padilla Bay was in part resource based.

Resource-controlled eelgrass growth during our experiments in Padilla Bay cannot be evaluated without consideration of the higher order effects that existed concurrently. Our laboratory experiments demonstrated that epiphytes have the potential to control eelgrass growth when the dominant mesoherbivore (Zdotea resecata) is absent, when nitrogen in the water column is abundant (>15 μmol/L combined inorganic nitrogen), and when temperatures are suboptimal (10°C) for eelgrass growth and leaf turnover (Tables 5 and 7, Figs. 5 and 6). This potential was not realized in the field experiments probably because of the combined effects of herbivory, low nitrogen availability in the water column, and optimal temperatures for eelgrass growth. Padilla Bay is relatively pristine and nitrogen availability in the shallow waters where eelgrass grows is always low (Fig. 4; Wissmar 1986). Nutrients are abundant entering the bay through sloughs and also in the deeper neritic and marine waters but most of the land-derived nutrients apparently are intercepted by the benthic plant communities of the marshes and mudflats before reaching the eelgrass beds (Wissmar 1986).

Our experiments help to define, for a given temperature and grazing intensity, the critical level of nutrient availability above which herbivory cannot control epiphyte biomass accumulation. Epiphyte biomass can accumulate linearly with increasing nitrogen availability in the water column up to at least 66 μmol/L (combined inorganic nitrogen), with negative impacts on eelgrass growth (Figs. 5 and 6, Table 7). In Padilla Bay, nitrogen concentrations in the water column were well within this range and also were at or below the half-saturation constants for nitrogen uptake by coastal microalgae (Goldman and Glibert 1983) and macroalgae (Hanisak 1983). Given this and that the doubling times (3–6 d; Borum 1987) for epiphyte biomass were within the duration of our experiments, epiphyte biomass should have been correlated with nitrogen availability in the water column and should have increased in response to our field fertilizations, yet it did not respond as predicted.

Table 8. Predicted conditions that limit growth of eelgrass (*Zostera marina*) at Padilla Bay, Washington.

Temperature <10°C (**Setchell** *1929)*
or
Sediment ammonium concentrations <500 μmol/L (Fig. *2)*
or
Light $<$*100* pmol of photons$\cdot m^{-2}\cdot s^{-1}$ *at the leaf surface* for $<$***6-8*** h daily (Dennison and Alberte *1985) when:*
  ambient light is low
  or
  epiphyte biomass is high *when:* water column $N_{inorganic}$ $>$*15* μmol/L and grazing intensity is low

The experimental results can be reconciled with predicted results if herbivory by Zdotea resecata is also considered. In the laboratory, at a higher combined inorganic nitrogen concentration (15 μmol/L) than measured in the field, *I.* resecata substantially reduced epiphyte biomass even when eelgrass leaf turnover was relatively slow (Table 5). In the winter when *I.* resecata are smaller and less abundant and nitrogen availability is maximal, light probably controls epiphyte biomass, as suggested elsewhere (Borum and Wium-Andersen 1980, Jacobs et al. 1983, Borum et al. 1984, Borum 1985, Thom and Albright 1990). Seasonal shifts in the relative importance of resource vs. higher order effects on eelgrass growth undoubtedly occur, as suggested by the difference in the results of the field fertilization study between sampling dates and from the diffuser experiment conducted in winter. This study only begins to define the boundary conditions that determine the relative importance of resource-based vs. higher order effects on eelgrass growth (Table 8).

Understanding the control of eelgrass growth is important for assessment of coastal primary production and management of the economically valuable eelgrass habitat. For example, estimation of herbivore control of epiphytes as a function of nitrogen loading rates is critical for management of eelgrass in Puget Sound because salmon net-pen aquaculture that can produce nutrient inputs equivalent to the treated sewage of a small city is being considered. The effects of herbivores or sediment nutrient sources are rarely considered in the evaluation of the environmental impact of such plans.

We demonstrated that edaphic factors (sediment nitrogen availability) combine with higher order effects of herbivores on putative competitors (epiphytes) to control eelgrass growth and that extrapolation from the effects of a single factor or season will not lead necessarily to correct predictions of the response of eelgrass in nature. A recent model ofeelgrass growth (Zimmerman et al. 1987) used light and nutrient availability in the water column and sediments to predict that nitrogen limitation was very unlikely. Padilla Bay is representative of dense intertidal eelgrass beds (McRoy and McMillan 1977, Phillips 1984, Thayer et al. 1984, Dennison et al. 1987) in terms of productivity (Table 4), shoot density (1250–5063 shoots/m^2; S. L. Williams, unpublished data), and dry biomass (150–180 g/m^2; Thom 1988), and exceeds all the critical conditions above which nitrogen limitation was not predicted by the model of Zimmerman et al. (1987). In spite of model predictions, eelgrass growth was nitrogen limited at least in April 1988. One explanation for the discrepancy between the model prediction and the empirical test is that epiphytes modify the light and nutrient environment at the leaf surface. At the scale relevant to the physiology of eelgrass, the microenvironment is quite different from that in the surrounding waters (Sand-Jensen 1977, Sand-Jensen et al. l985), upon which conditions the model was based.

Except for some tropical green macroalgae (Williams 1984), seagrasses are unique among marine plants in obtaining nutrients from both water column and sediment sources. The ability to utilize both nutrient sources in a complex habitat provides eelgrass with at least a partial release from nutrient competition with epiphytes that have more efficient uptake kinetics (Carpenter and Capone 1983, Thursby and Harlin 1982, Wallentinus 1984). Thus, eelgrass can persist through seasons of nutrient depletion in the water column, when epiphyte growth is likely to be limited (Borum 1985). Eelgrass also must be able to persist under heavy epiphyte loads until summer, when epiphytes are reduced as grazing intensifies the water column nutrients become depleted. The belowground biomass of eelgrass may enable it to persist during periods of light reduction due to increased epiphyte loads by providing a soluble carbohydrate reserve (Drew 1980) and nutrients when those in the water column are depleted. The effectiveness of the competitive release offered by the belowground biomass of eelgrass will depend on nutrient remineralization rates and concentrations in the sediments and on epiphyte-mediated attenuation of light because ammonium uptake and assimilation by eelgrass roots are light dependent (Smith et al. 1984, 1988, Pregnall et al. 1987).

Epiphyte loads in turn are determined in part by herbivory. Idotea resecata is a conspicuous mesoherbivore in a suite of many others in Padilla Bay (Simenstad et al. 1979, 1988). Species of Idotea have been implicated as major herbivores in other eelgrass systems and recently have been shown to consume more plant material in Padilla Bay than caprellid amphipods and a gastropod (R. M. Thom, unpublished data). Although the effect of Idotea on epiphytes was dramatic in our study, smaller grazers undoubtedly also reduce epiphytism (Caine 1980, Howard 1982, D'Antonio 1985, Brawley and Fei 1987) and partitioning the relative effects of meso- and microherbivores in eelgrass beds will require further manipulations. To this end, the cholinesterase inhibitor, I-naphthyl N-methylcarbamate, has no effect on the growth of Zostera marina and thus, may be useful in future grazing experiments (S. L. Williams, unpublished data).

In Padilla Bay, Idotea spp. do not appear in the guts of some fishes that forage in the eelgrass beds (Simenstad et al. 1988); however, they are preyed upon by shiner (Cymatogaster aggregata) and striped perch (Emiotoca lateralis) (R. M. Thom, unpublished data) and possibly numerous other fishes (sculpins, kelp greenlings, gunnels) and birds (blue herons and diving ducks) that utilize the seagrass beds (Simenstad et al. 1979). Here again habitat complexity impinges upon species interactions in eelgrass beds because mobile mesoherbivores and their predators select dense seagrass cover in response to predation and food availability (Stoner 1980, Leber 1985, Steffe et al. 1989). In the laboratory at unnaturally high densities, isopods damage eelgrass. If the natural predators of isopods are removed from the system, their effect on eelgrass may change from being beneficial to deleterious. Overgrazing of kelp by amphipods following reductions in fish predation after an El Niiio event in California provides a recent example of the importance of higher order interactions for understanding plant population dynamics (Tegner and Dayton 1987). Whether removal of isopod predators in Padilla Bay would cause a classic "trophic cascade" (Strong 1992) in which the herbivores then would consume eelgrass catastrophically, or alternatively, that the herbivores are controlled more by recruitment processes or food availability, remains to be tested. Although our study is limited in addressing the number of higher order interactions among consumers, it does suggest that feedback between consumers and resources (Power 1992), here between herbivores and resources as mediated by epiphytes that modify the leaf microenvironment, needs to be incorporated into theoretical models on the relative importance of resource or higher order control of plant productivity. Likewise, differing patterns of resource utilization (here, sediment vs. water nutrients) are important to identify. As suggested by Hunter and Price (1992), Power (1992), and Strong (1992), ecological complexity in Padilla Bay (functionally different, coexisting primary producers, unequal access to resources in the habitat, seasonality in primary productivity and grazing intensity, and indirect linkages between consumers and resources) may prevent catastrophic grazing on eelgrass (trophic cascade effect) even in the absence of predation on herbivores.

ACKNOWLEDGMENTS

We thank the director, T. Stevens, and staff of the Padilla Bay National Estuarine Research Reserve and Dr. A. O. Dennis Willows, director of Friday Harbor Laboratories, for facilitation of our research. Dr. W. C. Dennison provided us with some diffusers. L. Melly and L. Muehlstein slogged through much mud to assist us. We are indebted to our husbands, B. Nyden and S. Shabb, for assistance and understanding. J. Kershaw (Center for Quantitative Science, University of Washington) provided statistical consultation. Comments made by R. Paine, C. Simenstad, R. Thom, and reviewers (anonymous and T. Turner) improved our manuscript. Simenstad and Thom generously shared their wealth of experience and unpublished data from Padilla Bay. This research was supported by contract number NA87AA-D-CZ-009 from NOAA (to S. L. Williams) and matching funds were provided by Friday Harbor Laboratories of the University of Washington.

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