

# Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary

Scott T. Larned<sup>1,2,\*</sup>

<sup>1</sup>Coastal Ecology Branch, United States Environmental Protection Agency, 2111 SE Marine Science Drive, Newport, Oregon 97365, USA

<sup>2</sup>Present address: National Institute of Water and Atmospheric Research, PO Box 8602, Christchurch, New Zealand

**ABSTRACT:** The effects of *Z. japonica* on dissolved nutrient fluxes between the water column and the benthos in Yaquina Bay, Oregon, USA were examined. Nutrient fluxes in *Zostera japonica* habitats were compared to those in adjacent unvegetated sediment in warm and cool seasons, and in daylight and darkness. In daylight, *Z. japonica* habitats were net sinks for nitrate (NO<sub>3</sub>), ammonium (NH<sub>4</sub>) and dissolved reactive phosphorus (DRP) in the warm season, and for NO<sub>3</sub> and DRP in the cool season. At night in the warm season, *Z. japonica* habitats were net sinks for NO<sub>3</sub> and NH<sub>4</sub>. Unvegetated sediments were net sources of NH<sub>4</sub> to the water column in daylight in both seasons, and net sinks for NO<sub>3</sub> at night in the warm season. On a diel basis, *Z. japonica* habitats were net sinks for NO<sub>3</sub> and NH<sub>4</sub>, and unvegetated sediments were net sources of NH<sub>4</sub>. Porewater NO<sub>3</sub> and NH<sub>4</sub> concentrations in unvegetated sediments were twice those in *Z. japonica* habitats. Nutrient fluxes in abutting monospecific patches of *Z. japonica* and the native seagrass *Z. marina* were also compared. Both species were sinks for NO<sub>3</sub>, NH<sub>4</sub> and DRP. NO<sub>3</sub> influx rates per unit above-ground biomass were higher in *Z. japonica* habitats, but areal rates of NO<sub>3</sub> influx were higher in *Z. marina* habitats, reflecting the latter's higher biomass. The data demonstrate that *Z. japonica* invasions alter water column-benthos nutrient fluxes. These alterations may in turn affect pelagic primary production. At current biomass levels, *Z. japonica* is estimated to remove 50 to 60 mole dissolved inorganic nitrogen (DIN) h<sup>-1</sup> and 0.2 to 2.2 mole DRP h<sup>-1</sup> from the Yaquina Bay water column, and continued expansion of *Z. japonica* in the estuary could lead to substantial reductions in nutrient availability.

**KEY WORDS:** Estuary · Invasion · Nonindigenous species · Nutrient flux · NE Pacific · Porewater · Seagrass · Sediment · *Zostera japonica*

Resale or republication not permitted without written consent of the publisher

## INTRODUCTION

Invasions of estuaries by nonindigenous plants are increasing in frequency and geographic extent (Eno 1996, Cohen & Carlton 1998, Ruiz et al. 1999). Aquatic plant invasions can alter nutrient cycling, primary production, and other ecosystem processes (Gordon 1998, Rooth & Stevenson 2000). Once established, many nonindigenous aquatic plants have proven too costly to eradicate, which may preclude the restoration of normal ecosystem functions (Turner et al. 1998). Quantitative studies of the effects of nonindigenous estuarine

species are rare; Ruiz et al. (1999) estimated that in the best-studied estuaries, the effects of fewer than 5% of the nonindigenous species have been measured. Some of these studies have linked changes in nutrient cycling in estuarine oligohaline zones to nonindigenous plants (e.g. Posey et al. 1993, Templer et al. 1998, Meyerson et al. 1999). In contrast, the effects of nonindigenous plants on nutrient cycling in lower (mesohaline and marine) estuary zones have not been reported. In light of the effects that nonindigenous plants have had in oligohaline zones, similar changes may be expected when mesohaline and marine zones are invaded.

\*Email: s.larned@niwa.co.nz

Seagrasses are major sinks and sources of dissolved nutrients in mesohaline and marine estuary zones (Pérez-Lloréns et al. 1993, Hemminga et al. 1994, Risgaard-Petersen et al. 1998, Hansen et al. 2000, Welsh et al. 2000). The dominant role of native seagrasses in nutrient cycling raises the possibility that the establishment of a nonindigenous seagrass would alter nutrient source-sink patterns in the invaded estuary. Such changes could affect sediment chemistry, and benthic and pelagic productivity.

The intertidal seagrass *Zostera japonica* Aeschers. & Graebn. was introduced to NW North America from eastern Asia in the early to mid-20th century, possibly in shipments of Japanese oysters imported for mariculture (Harrison & Bigley 1982). By the 1980s, *Z. japonica* was established in several estuaries between the southern Strait of Georgia and Coos Bay, Oregon (Harrison & Bigley 1982, Posey 1988). By 1999, *Z. japonica* was present in most estuaries between Powell River, British Columbia and Coquille River, Oregon (author's pers. obs.).

In invaded estuaries of the NE Pacific, *Zostera japonica* forms dense patches in the intertidal zone, 0.3 to 2.4 m above mean lower low water (MLLW) (Harrison & Bigley 1982, Posey 1988, Thom 1990). In the absence of *Z. japonica*, this zone is often unvegetated. Following colonization by seeds or asexual propagules, *Z. japonica* patches increase in size through rhizome growth and may expand at rates

>100% mo<sup>-1</sup> during the spring and summer growing season (Harrison & Bigley 1982). Throughout its range in the NE Pacific, *Z. japonica* co-occurs with the native seagrass *Zostera marina* L. *Z. marina* occupies an elevation zone below that of *Z. japonica*, from ~0.5 m above MLLW to subtidal depths, and there is generally an unvegetated band between the 2 seagrasses. At some sites, the lower extent of *Z. japonica* and the upper extent of *Z. marina* overlap, and the seagrasses form mixed patches and abutting monospecific patches (Thom 1990, Nomme & Harrison 1991a).

In this study, I examined the effects of *Zostera japonica* on dissolved nutrient fluxes between the water column and the benthos in Yaquina Bay, Oregon. Areas of unvegetated sediment between *Z. japonica* patches served as reference sites for assessing the effects of the seagrass. At locations where abutting monospecific patches of *Z. japonica* and *Z. marina* occurred, I compared the effects of the nonindigenous and native seagrasses on nutrient fluxes. *Z. japonica*, *Z. marina* and unvegetated sediments were determined to be net sources or sinks for nitrate (NO<sub>3</sub>), ammonium (NH<sub>4</sub>) and dissolved reactive phosphate (DRP) based on patterns of influx or efflux. The terms influx and efflux refer to nutrient removal from the water column, and nutrient release to the water column, respectively. Nutrient fluxes represent the net effects of entire benthic assemblages, e.g. seagrasses, epiphytic and benthic algae, sediments and sediment fauna. For brevity, the benthic assemblages associated with unvegetated sediments and with *Z. japonica* and *Z. marina* are referred to hereafter as 'habitats'.

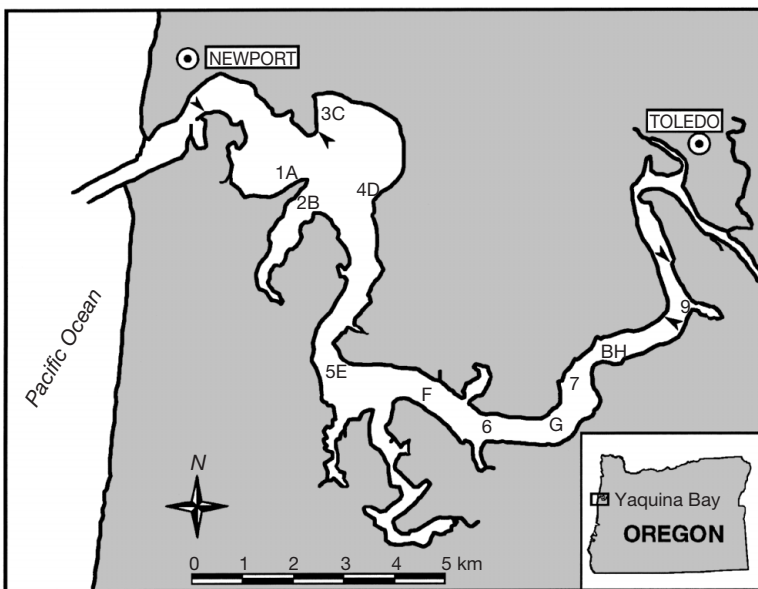


Fig. 1. Map of Yaquina Bay, central coast of Oregon. Numbers: locations of nutrient-flux experiments; letters: locations of permanent transects used to monitor *Zostera japonica* biomass. Arrowheads indicate upstream and downstream range limits of *Z. japonica* on north and south shores of Yaquina Bay in spring 2001

## MATERIALS AND METHODS

**Study sites.** The study was carried out in Yaquina Bay (44.6°N, 124.0°W), a drowned-river estuary on the central coast of Oregon. The combined area of marine and mesohaline zones in Yaquina Bay is 18 km<sup>2</sup>, of which ~40% is subtidal channel and 60% is intertidal mudflat, sandflat, and seagrass habitat. At the time the study was conducted, *Zostera japonica* covered <5% of the intertidal area. *Z. japonica* occurs between 0.5 and 2 m above MLLW in Yaquina Bay. The longitudinal distribution extends for 18 km, from the mixing zone near the mouth of Yaquina Bay at Newport through the mesohaline zone near Toledo (Fig. 1). Individual *Z. japonica* patches range in area from <1 to >500 m<sup>2</sup>. Unvegetated areas adjacent to *Z. japonica* patches are

frequently inhabited by dense populations of the thalassinid shrimp *Neotrypaea californiensis* Dana and *Upogebia pugettensis* Dana.

**Nutrient flux experiments.** Three experiments were conducted. Expt 1 was a comparison of nutrient fluxes in *Zostera japonica* and unvegetated sediment habitats in the warm and cool seasons. Nutrient flux measurements were made at locations spanning the longitudinal range of *Z. japonica* in the estuary (Fig. 1). Warm and cool seasons were delineated using sediment temperature data. Temperature loggers (Onset Corporation, TidbiT loggers) were continuously deployed from July 1999 to June 2000 in *Z. japonica* patches at 5 cm sediment depth at 1 of the study locations, and average daily temperatures were computed from the logger data. Lowest daily temperatures (3 to 4°C) were in January, highest daily temperatures (19 to 20°C) were in August, and the median daily temperature (10.6°C), was in March and October. These data were used to divide the study period into a warm season (May to September 1999) and a cool season (January to April 2000). Nutrient flux measurements were made at 9 locations in the warm season and repeated at 5 locations in the cool season.

Expt 2 addressed the possibility that nutrient fluxes in *Zostera japonica* and unvegetated sediment habitats are light-dependent, and exhibit diel patterns. Paired day-night experimental runs were conducted at 4 locations from May to August 1999 to compare nutrient flux rates in daylight and in darkness. The locations used for this experiment were also used for Expt 1, but different *Z. japonica* and unvegetated sediment patches were used.

Expt 3 was a comparison of nutrient fluxes associated with the native and nonindigenous seagrasses. Nutrient flux measurements were made from April to June 2000 in abutting *Zostera japonica* and *Z. marina* patches at 3 locations. At each site, the seagrass patches were at the same tidal elevation. The locations used for this experiment were also used for Expt 1, but different *Z. japonica* patches were used.

Nutrient fluxes were measured using benthic chambers. Chambers were installed in 2 pieces to minimize sediment disturbance. The first piece, a 42 cm diameter × 10 cm long PVC coupler, was inserted in the sediment 4 to 5 d before the experiment, with the top edge flush with the sediment surface. The second piece, a 41 cm diameter × 40 cm long PVC pipe with a clear acrylic lid, was installed immediately before the experiment by holding it underwater to fill with seawater, then inserting it into the top edge of the coupler. The chambers enclosed 1140 cm<sup>2</sup> of substratum and 46 l of seawater. A large volume:area ratio (0.4 m<sup>3</sup> m<sup>-2</sup>) was used to minimize the effect of changing nutrient concentrations on diffusive fluxes (Forja & Gomez-

Parra 1998). The acrylic lids were equipped with battery-operated 70 rpm stirrers, and sampling and incurrent ports for withdrawing and replacing water. Stirrer propellers were trimmed to length to ensure that the water in chambers was mixed from top to bottom without sediment suspension.

During each run of Expts 1 and 2, 2 benthic chambers were installed over *Zostera japonica* and 2 over unvegetated sediment. During each run of Expt 3, 2 chambers were installed over *Z. japonica* and 2 over *Z. marina*. Chambers were installed parallel to the shoreline, ~2 m apart, without regard for the density of underlying seagrass. In all runs, a fifth chamber was used as a control for nutrient fluxes in the water column. The control chamber had a closed bottom, otherwise it was identical to the open-bottomed chambers. After the open-bottomed chambers were installed, the control chamber was filled with water from the study site, and placed in a 100 l water bath. The water in the bath was continuously replaced with estuary water to maintain the chamber at ambient temperatures. Experimental runs were 4 to 7 h long, and spanned the high slack tide. In Expt 2, nighttime measurements were made first, the PCV couplers were left in place at the end of the run, and the chambers were replaced in the couplers on the following day for the daylight measurements.

Water samples were collected from the chambers by attaching a syringe to the sampling port, opening the incurrent port, withdrawing and discarding 60 ml of water to rinse the port and syringe, then withdrawing and retaining 60 ml of water. Less than 2% of the chamber volume was replaced during an experimental run. Water samples were collected at 30 to 120 min intervals, and were filtered immediately through GF/F filters into HCl-washed Nalgene bottles, placed on ice, then frozen in the laboratory until analysis. Nutrient concentrations were determined using a Lachat Instruments QwikChem 8000 analyzer at Analytical Laboratory, University of California Santa Barbara. Nutrient flux rates ( $\mu\text{mol m}^{-2} \text{h}^{-1}$ ) were calculated from linear regressions of nutrient concentration on elapsed time during the first 3 to 5 h of the experiment runs. Rates of change in nutrient concentrations in the control chamber were used to correct water column-benthos flux rates from the same experimental run. Nitrite (NO<sub>2</sub>) concentrations in ambient water samples were always <5% of NO<sub>3</sub> concentrations, and NO<sub>2</sub> fluxes are not reported here. Irradiance (photosynthetically active radiation) was measured next to the chambers, 10 cm above the substrate, during daylight runs using a Li-Cor LI 192SA sensor and a LI 250 meter. The acrylic chamber lids reduced irradiance in the chambers by 10 to 15%.

**Sediment, seagrass and porewater samples.** Core samples of sediments and *Zostera japonica* or *Z. marina*

tissues enclosed by the benthic chambers were collected during the low tide following each run of Expts 1 and 3. Three sizes of cores were collected during Expt 1: large (8 cm diameter  $\times$  15 cm deep) cores for seagrass biomass measurement, medium (3.5 cm diameter  $\times$  15 cm deep) cores for particulate nutrient and grain size analysis, and small (3.1 cm diameter  $\times$  2 cm deep) cores for sediment chlorophyll *a* analysis. Sediment chlorophyll cores were not collected during Expt 3. Three replicate cores of each size were collected from the area beneath each chamber, and the data from replicate cores were averaged and treated as single samples in subsequent analyses.

In the laboratory, seagrass biomass cores were rinsed of sediment over a 0.5 mm mesh sieve, then above-ground (shoots, leaves, inflorescences) and below-ground (roots and rhizomes) portions were separated, dried to constant weight at 70°C, ashed at 500°C for 4 h and reweighed for ash-free dry weight (AFDW) determination. The medium cores were homogenized, then divided into 3 portions: ~150 g wet weight for sediment grain size analysis, 20 g for particulate organic carbon (POC) and particulate nitrogen (PN) analyses, and the remainder for particulate phosphorus (PP) analysis. Sediment grain size analysis followed Buchanan (1984). Combined sieve and pipette analyses were used to determine dry weights of 7 grain size classes (4.0, 2.0, 1.0, 0.5, 0.25, 0.125 and 0.063 mm, silt and clay). Mean grain sizes and sorting coefficients (arithmetic standard deviations) were calculated from grain size frequency distributions. POC and PN concentrations were measured with a Perkin Elmer 2400 elemental analyzer, PP concentrations were measured with an Alpkem rapid flow analyzer. The small cores for chlorophyll *a* analysis were transferred to centrifuge tubes. Cold 90% acetone was added to each tube, the sediment-acetone mixture was sonicated, and chlorophyll was extracted for 48 h in darkness at 0°C. The tubes were then centrifuged and chlorophyll *a* concentrations in the supernatants were measured with a Turner Design AU-10 fluorometer.

Porewater samples were taken from the sediment 20 cm from the benthic chambers. Porewater samplers were made from 10 cm lengths of 2.5 cm diameter PVC tube with caps on both ends. Two 10 cm Tygon tubes were inserted in holes in one of the caps. Slots were cut into the PVC tubes at 0.5 cm intervals, and the tubes were wrapped in Nitex screen (200  $\mu$ m mesh) to allow solute exchange. Two or 3 samplers were installed near each benthic chamber base 4 to 5 d before the experimental run. The samplers were inserted vertically in 20 cm deep holes with the Tygon tubes protruding, and then filled with deionized water. Porewater samples were collected at low tide 7 to 10 d after the experimental run by withdrawing water with a syringe

through one of the Tygon tubes. The second tube allowed air to displace sample water and prevented contamination with surrounding water. Porewater samples were processed for nutrient analysis as described above for benthic chamber samples. No porewater samples were collected during Expt 2.

**Biomass monitoring.** Permanent transects were established at 8 locations with large *Zostera japonica* patches (long axis >40 m length) to monitor temporal changes in *Z. japonica* biomass. These locations spanned the longitudinal range of *Z. japonica* in Yaquina Bay (Fig. 1). At each location, a 40 m long transect was established parallel to the water line, bisecting the *Z. japonica* bed. Core samples (8 cm diameter  $\times$  15 cm deep) were collected at 12 random points on each transect at 2 mo intervals for 22 mo (February 1999 to December 2000). The above- and below-ground biomass of *Z. japonica* in the cores was determined as described above.

**Data analyses.** Nutrient flux rates in *Zostera japonica* and unvegetated sediment habitats in the warm and cool seasons (Expt 1), and in daylight and darkness (Expt 2) were compared by factorial ANOVA. For Expt 3, nutrient fluxes in *Z. japonica* and *Z. marina* habitats were compared by 1-way ANOVA. The normality of flux rate data was assessed using linear correlations of the flux rates for each treatment, with normal scores calculated from the same data. Correlation coefficients were  $\geq 0.9$  in each case. Locations of experimental runs were used as blocks in ANOVAs. Time constraints prevented experimental runs from being conducted simultaneously at each location during each experiment, so runs were conducted at a different location every 6 to 18 d during each season. This approach risked confounding effects of locations with short-term temporal variability, i.e. dates within seasons. However, among-location differences in nutrient fluxes were generally larger than between-season differences (see 'Results'), and it was assumed that among-location differences were also greater than among-date differences.

The data from Expt 2 were used to estimate diel nutrient flux rates. The following assumptions were made: (1) water column-benthos nutrient flux only occurred when the study sites were immersed, not when they were emersed; (2) study sites were immersed at tidal heights  $\geq 1.25$  m above MLLW. This height corresponds to the center of the tidal range of *Zostera japonica*; (3) daylight periods were from local sunrise to local sunset, and dark periods were from sunset to sunrise. Average hours of immersion in daylight and darkness per day were taken from tidal predictions for Yaquina Bay at Newport, Oregon, using the WWW Tide and Current Predictor (available at [http://tbone.biol.sc.edu/tide/sites\\_uswest.html](http://tbone.biol.sc.edu/tide/sites_uswest.html)). Diel

fluxes were estimated as mean daytime flux rates multiplied by the immersed daylight period plus mean nighttime flux rates multiplied by the immersed dark period.

Seagrass and unvegetated sediment habitats were determined to be net sinks or net sources of each nutrient based on 95% confidence intervals (CI) around the mean flux rates. If a mean  $\pm$  CI flux rate was  $>0$ , the habitat was considered a net source; if a mean  $\pm$  CI flux rate was  $<0$ , the habitat was considered a net sink.

To quantify relationships between nutrient fluxes and seagrass biomass, flux rates were regressed on the seagrass biomass enclosed by the benthic chambers. Separate linear regressions were calculated for *Zostera japonica* in the warm and cool seasons (Expt 1) and for *Z. japonica* and *Z. marina* in the warm season (Expt 3). Associations between nutrient fluxes in the *Z. japonica* habitat and a suite of chemical and physical variables (ambient nutrient concentrations, sediment properties, temperature and irradiance) were examined by correlation analysis. Variable values used in correlations were means from the experimental runs.

Chemical and physical properties of sediments in adjacent *Zostera japonica* patches and unvegetated sediments in both seasons were compared by factorial ANOVA (Expt 1). Sediment properties in adjacent *Z. japonica* and *Z. marina* patches were compared by 1-way ANOVA (Expt 3).

## RESULTS

### Ambient conditions and control chambers

Experimental runs were conducted over a temperature range of 6 to 22°C, and a salinity range of 16 to

33‰. Water temperatures during the warm season runs of Expt 1 were always higher than in the cool season runs (Table 1). During some runs, a lens of brackish water was present when the chambers were filled on the rising tide, and salinity in the benthic chambers was then lower than the average salinity outside the chambers. Mean irradiance during daytime runs ranged from 126  $\mu\text{E m}^{-2} \text{s}^{-1}$  in the cool season to 429–510  $\mu\text{E m}^{-2} \text{s}^{-1}$  in the warm season (Table 1).  $\text{NO}_3$  was the dominant form of inorganic nitrogen in the water column; ambient  $\text{NO}_3$  concentrations were 3 to 17 $\times$  higher than  $\text{NH}_4$  concentrations and 40 to 180 $\times$  higher than  $\text{NO}_2$  concentrations (Table 1). Elevated  $\text{NO}_3$  and SiO concentrations during the cool season portion of Expt 1 reflect dissolved nutrient loading to Yaquina Bay from the Yaquina River during high winter flows (Table 1).

Nutrient fluxes in the water column were measured during each experiment run using the control chamber. Rates of  $\text{NO}_3$ ,  $\text{NH}_4$ , and DRP flux in the control chamber were always less than 10% of the rates in chambers installed over seagrass and unvegetated sediment habitats. For each nutrient in each experiment, 95% confidence intervals for mean flux rates in the controls included zero, indicating that the water column was not a significant sink for or source of inorganic nutrients.

### Expt 1. Nutrient fluxes in *Zostera japonica* and unvegetated sediment habitats

*Zostera japonica* habitats were net sinks for  $\text{NO}_3$ ,  $\text{NH}_4$ , and DRP during the warm season, and net sinks for  $\text{NO}_3$  and DRP during the cool season (Fig. 2a).  $\text{NH}_4$  fluxes in *Z. japonica* habitats in the cool season were

Table 1. Water temperature, irradiance, salinity and ambient nutrient concentrations during benthic chamber experiments. Values are means  $\pm$  1 SD; sample sizes in parentheses. nm: no measurement. DRP: dissolved reactive phosphorus

Experiment	Temperature (°C)	Irradiance ( $\mu\text{E m}^{-2} \text{s}^{-1}$ )	Salinity (‰)	Ambient concentration ( $\mu\text{M}$ )				
				$\text{NO}_3$	$\text{NH}_4$	DRP	$\text{NO}_2$	SiO
<b>Expt 1</b>								
Warm season	15.7 $\pm$ 2.2 (40)	429 $\pm$ 565 (36)	26.1 $\pm$ 5.7 (40)	7.9 $\pm$ 5.3 (9)	2.9 $\pm$ 1.0 (9)	1.0 $\pm$ 0.5 (9)	0.2 $\pm$ 0.1 (9)	58.7 $\pm$ 17.5 (9)
Cool season	8.6 $\pm$ 1.4 (26)	126 $\pm$ 209 (15)	21.9 $\pm$ 6.5 (26)	35.4 $\pm$ 20.2 (5)	2.3 $\pm$ 0.5 (5)	0.7 $\pm$ 0.2 (5)	0.2 $\pm$ 0.0 (5)	86.9 $\pm$ 20.6 (5)
<b>Expt 2</b>								
Daytime	16.0 $\pm$ 4.3 (16)	510 $\pm$ 427 (16)	26.6 $\pm$ 7.3 (16)	8.1 $\pm$ 8.0 (4)	2.5 $\pm$ 0.8 (4)	0.8 $\pm$ 0.5 (4)	0.1 $\pm$ 0.1 (4)	54.1 $\pm$ 19.2 (4)
Nighttime	15.5 $\pm$ 2.6 (18)	nm	25.8 $\pm$ 4.9 (18)	9.1 $\pm$ 3.6 (4)	2.2 $\pm$ 0.1 (4)	1.13 $\pm$ 0.26 (4)	0.3 $\pm$ 0.0 (4)	48.4 $\pm$ 15.4 (4)
<b>Expt 3</b>								
	14.1 $\pm$ 2.2 (16)	383 $\pm$ 240 (12)	25 $\pm$ 7.0 (16)	13.7 $\pm$ 3.8 (3)	2.8 $\pm$ 1.1	0.63 $\pm$ 0.20 (3)	0.2 $\pm$ 0.1 (3)	58.2 $\pm$ 4.3 (3)

too variable to determine the net direction, i.e. the 95% CI for the mean flux rate included zero. Rates of  $\text{NO}_3$  flux in *Z. japonica* habitats were on average 5× greater than  $\text{NH}_4$  flux rates. Unvegetated sediments were sources of  $\text{NH}_4$  to the water column in both seasons (Fig. 2a).  $\text{NO}_3$  and DRP fluxes associated with unvegetated sediments were too variable to determine net directions.

$\text{NO}_3$  and  $\text{NH}_4$  flux rates in *Zostera japonica* habitats were significantly higher than in unvegetated sediments (Table 2). Between-habitat differences in DRP fluxes were not significant. In the warm season,  $\text{NH}_4$  and DRP flux

Table 2. Expt 1. Summaries of factorial ANOVAs comparing flux rates of  $\text{NO}_3$ ,  $\text{NH}_4$ , DRP, and in *Zostera japonica* and unvegetated habitats in 2 seasons (warm vs cool). 'Blocks' = locations in Yaquina Bay

Source	df	$\text{NO}_3$		DRP		$\text{NH}_4$	
		MS	p	MS	p	MS	p
Habitat	1	442 867.2	<0.001	116 042.8	<0.001	124.4	0.45
Season	1	60 275.5	0.08	23 084.1	0.03	649.7	0.05
Interaction	1	178.0	0.92	5135.8	0.32	84.7	0.53
Blocks	8	96 701.4	<0.001	28 185.6	<0.001	400.8	0.06
Error	44	43 734.4		4692.7		200.3	

rates in *Z. japonica* habitats were twice as high as in the cool season (Fig. 2a). These differences were significant, but the main effect of season on  $\text{NO}_3$  flux rates was not significant (Table 2). Differences among locations in Yaquina Bay ('Blocks' in Table 2) were significant for each nutrient. The among-location variability in nutrient fluxes prevented the determination of net flux directions in each habitat and season.

$\text{NO}_3$  influx rates in *Z. japonica* habitats increased with increasing above-ground seagrass biomass in both seasons (Table 3). The slope of the regression for the warm season was significantly steeper than for the cool season, i.e.  $\text{NO}_3$  influx per unit above-ground biomass was greater during the warm season (Student's *t*-test of slopes,  $t = 2.35$ ,  $df = 25$ ,  $p < 0.05$ ). Regressions of  $\text{NH}_4$  and DRP flux rates on above-ground biomass, and regressions of all nutrient flux rates on below-ground biomass were not significant.

Porewater  $\text{NO}_3$  and  $\text{NH}_4$  concentrations were twice as high, and sediment chlorophyll *a* concentrations were 20% higher in unvegetated sediments than in *Zostera japonica* habitats (Table 4). These between-habitat differences were significant (ANOVA,  $p < 0.05$ ). Smaller between-habitat differences in grain size, grain size heterogeneity and particulate nutrient concentrations were not significant (Table 4). There were significant between-season differences in several

Table 3. *Zostera japonica* and *Z. marina*. Regressions of nutrient flux rates ( $\mu\text{mol m}^{-2} \text{h}^{-1}$ ) on above-ground biomass ( $\text{g ash-free dry wt m}^{-2}$ ). Regressions had slopes significantly different from zero ( $p < 0.05$ )

Species Expt	Nutrient	Slope	Intercept	$R^2$
<i>Z. japonica</i>				
1 (warm season)	$\text{NO}_3$	-21.3	590.8	0.33
1 (cool season)	$\text{NO}_3$	-5.1	-12.7	0.27
3	$\text{NO}_3$	-4.6	2.7	0.68
<i>Z. marina</i>				
3	$\text{NO}_3$	-1.6	-97.6	0.83
3	DRP	0.07	-11.4	0.76

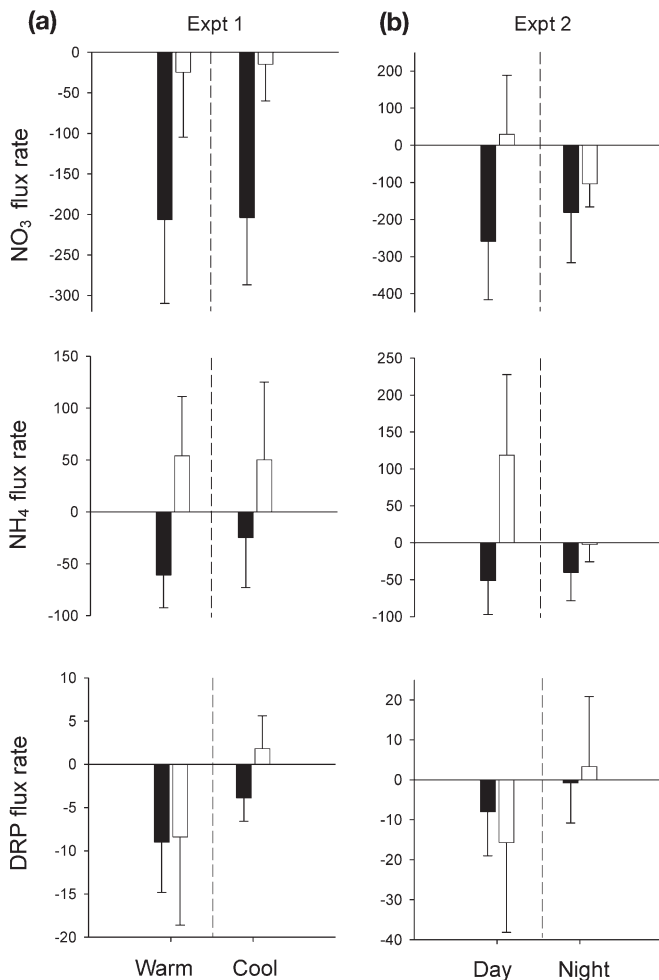


Fig. 2. Expts 1 and 2. Mean daytime nutrient flux rates in *Zostera japonica* habitats (black bars) and unvegetated sediment habitats (white bars), in (a) warm (May to August) and cool (January to April) seasons, and (b) in daylight and at night. Positive rates indicate efflux, negative rates influx; error bars = 95% CI. In (a)  $n = 18$  in warm season, 10 in cool season; in (b)  $n = 8$ . DRP: dissolved reactive phosphorus

Table 4. Expt 1. Sediment properties in *Zostera japonica* and unvegetated sediment habitats in warm and cool seasons. Values are means  $\pm$  1 SD. n = 18 in warm season, 10 in cool season except where shown in parentheses

Variable	<i>Z. japonica</i>		Unvegetated sediment	
	Warm	Cool	Warm	Cool
Mean grain size (mm)	0.3 $\pm$ 0.2	0.2 $\pm$ 0.1	0.3 $\pm$ 0.2	0.2 $\pm$ 0.1 (5)
Grain size heterogeneity (mm)	0.5 $\pm$ 0.3	0.4 $\pm$ 0.2	0.5 $\pm$ 0.4	0.4 $\pm$ 0.2 (5)
POC (% dry wt)	1.2 $\pm$ 0.9	1.4 $\pm$ 1.2	1.3 $\pm$ 1.0	1.4 $\pm$ 1.4 (5)
PN (% dry wt)	0.1 $\pm$ 0.1	0.3 $\pm$ 0.1	0.1 $\pm$ 0.1	0.2 $\pm$ 0.1 (5)
PP (% dry wt)	0.002 $\pm$ 0.001	0.002 $\pm$ 0.001	0.002 $\pm$ 0.0004	0.002 $\pm$ 0.001 (5)
Porewater NO <sub>3</sub> ( $\mu$ M)	0.8 $\pm$ 1.0	0.8 $\pm$ 1.8	1.2 $\pm$ 1.4	2.0 $\pm$ 3.7
Porewater NH <sub>4</sub> ( $\mu$ M)	66.1 $\pm$ 51.7	60.2 $\pm$ 61.1	97.6 $\pm$ 70.0	170.2 $\pm$ 104.5
Porewater DRP ( $\mu$ M)	3.29 $\pm$ 6.86	5.46 $\pm$ 12.92	4.26 $\pm$ 9.18	5.57 $\pm$ 8.24
Sediment chlorophyll <i>a</i> (mg m <sup>-2</sup> )	56.4 $\pm$ 16.4	61.7 $\pm$ 28.0	81.4 $\pm$ 29.2	67.0 $\pm$ 35.6

sediment variables: PN and porewater NO<sub>3</sub> and DRP concentrations were higher in the cool season, and mean grain sizes were larger during the warm season (Table 4).

### Expt 2. Day-night differences in nutrient flux rates

*Zostera japonica* habitats were net sinks for both NO<sub>3</sub> and NH<sub>4</sub> during the day and at night (Fig. 2b). Unvegetated sediments were net sinks for NO<sub>3</sub> at night, and net sources of NH<sub>4</sub> during the day (Fig. 2b). Nighttime NH<sub>4</sub> fluxes and daytime NO<sub>3</sub> fluxes in unvegetated sediments, and DRP fluxes in both habitats at both light levels were too variable to determine net directions.

There were significant differences in NH<sub>4</sub> fluxes between habitats and between light levels (Table 5). The habitat  $\times$  light interaction was also significant for NH<sub>4</sub>, because efflux from unvegetated sediments was rapid in daylight and decreased to near-zero at night, while NH<sub>4</sub> influx to *Zostera japonica* habitats in daylight was ~20% higher than at night (Fig. 2b). There was a significant between-habitat difference in NO<sub>3</sub> flux, and the habitat  $\times$  light interaction for NO<sub>3</sub> was significant, but the main effect of light was not significant (Table 5). The NO<sub>3</sub> interaction was also due to the large difference between habitats in daylight, and the smaller difference at night. Between-habitat and between light-level differences in DRP flux rates were not significant. Differences in flux rates among locations were significant for each nutrient.

On a diel basis, *Zostera japonica* habitats were net sinks for both NO<sub>3</sub> and NH<sub>4</sub>, and unvegetated sediments were net sources of NH<sub>4</sub> (Table 6). Diel rates of DRP flux in both habitats were too variable to determine net directions. Although unvegetated sediments were net NO<sub>3</sub> sinks at night, this pattern was offset by high variability in daylight, and the diel NO<sub>3</sub> fluxes were also too variable to determine net direction.

### Expt 3. Nutrient fluxes in *Zostera japonica* and *Z. marina* habitats

At locations where daytime nutrient flux measurements were made in adjacent *Zostera japonica* and *Z. marina* habitats, both species were net sinks for NO<sub>3</sub>,

Table 5. Expt 2. Summaries of factorial ANOVAs comparing flux rates of NO<sub>3</sub>, NH<sub>4</sub> and DRP in *Zostera japonica* and unvegetated sediment habitats at 2 light levels (daylight vs darkness). Experimental runs were from May to August 1999. Blocks = locations in Yaquina Bay

Source	df	NO <sub>3</sub>		DRP		NH <sub>4</sub>	
		MS	p	MS	p	MS	p
Habitat	1	267 909.8	0.002	86 405.8	<0.001	26.0	0.8
Light level	1	6356.4	0.6	24 294.2	0.04	1367.9	0.09
Interaction	1	88 574.8	0.06	34 737.9	0.017	279.8	0.4
Blocks	3	303 734.2	<0.001	20 832.7	0.019	1582.8	0.03
Error	25	23 596.6		5259.3		437.5	

Table 6. Expt 2. Diel fluxes of NO<sub>3</sub>, NH<sub>4</sub> and DRP in *Zostera japonica* and unvegetated sediment habitats ( $\mu$ mol m<sup>-2</sup> d<sup>-1</sup>). Values are means  $\pm$  95% CI; n = 8. Positive signs indicate efflux, negative signs influx

Habitat	NO <sub>3</sub>	NH <sub>4</sub>	DRP
<i>Z. japonica</i>	-1654.7 $\pm$ 1327.0	-338.9 $\pm$ 274.6	-38.2 $\pm$ 69.2
Unvegetated sediment	-143.9 $\pm$ 894.2	+530.3 $\pm$ 429.0	-62.0 $\pm$ 125.6

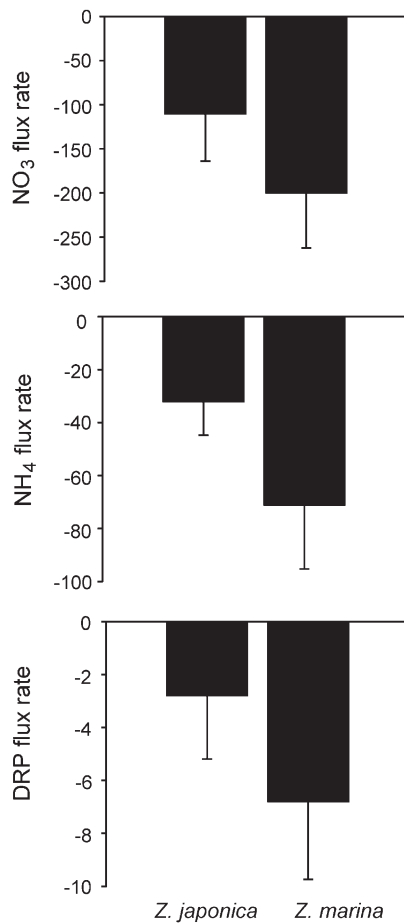


Fig. 3. Expt 3. Mean nutrient influx rates in *Zostera japonica* and *Z. marina* habitats. Error bars = 95% CI; n = 6

NH<sub>4</sub>, and DRP (Fig. 3). Mean rates of NO<sub>3</sub>, NH<sub>4</sub>, and DRP influx to *Z. marina* habitats were about twice the mean rates of influx to *Z. japonica* habitats. Differences between seagrass species in NH<sub>4</sub> and DRP influx rates were significant (ANOVA,  $p < 0.05$ ), and the difference in NO<sub>3</sub> influx rates was marginally significant ( $p = 0.064$ ).

NO<sub>3</sub> influx rates increased with above-ground seagrass biomass in both *Zostera japonica* and *Z. marina* habitats (Table 3). The slope of the NO<sub>3</sub> regression was steeper for *Z. japonica*, i.e. NO<sub>3</sub> influx per unit biomass was higher for *Z. japonica* habitats (Student's  $t$ -test of slopes,  $t = 3.42$ ,  $df = 8$ ,  $p < 0.01$ ). DRP influx decreased with increasing above-ground biomass in *Z. marina* habitats (Table 3). DRP flux rates were not related to above-ground *Z. japonica* biomass, and NH<sub>4</sub> fluxes were not related to above-ground biomass for either seagrass. Regressions using below-ground biomass were not significant. Differences between seagrass species in areal nutrient flux rates may have been due to differences in above-ground biomass at the study

locations. Mean above-ground biomass of *Z. marina* was 65.9 g AFDW m<sup>-2</sup>, compared with 24.6 g AFDW m<sup>-2</sup> for *Z. japonica*.

Mean sediment grain sizes, sediment heterogeneity, and porewater NH<sub>4</sub> concentrations were significantly higher in *Z. japonica* habitats than in *Zostera marina* habitats (Table 7, ANOVA,  $p < 0.03$ ). Differences between seagrass species in particulate nutrient and porewater NO<sub>3</sub> and DRP concentrations were not significant.

### Nutrient flux correlations and *Zostera japonica* biomass patterns

Associations between nutrient fluxes in *Zostera japonica* habitats and physical and chemical variables were identified by linear correlation, using data from all 3 experiments. Only coefficients for significant ( $p < 0.05$ ) correlations are reported. NO<sub>3</sub> flux was positively correlated with temperature ( $r = 0.71$ ) and ambient NO<sub>3</sub> concentration ( $r = 0.66$ ). NH<sub>4</sub> flux was positively correlated with irradiance ( $r = 0.68$ ) and ambient NH<sub>4</sub> concentration ( $r = 0.86$ ). DRP flux was positively correlated with temperature ( $r = 0.64$ ). No significant correlations between nutrient fluxes and sediment grain size structure, porewater or particulate nutrients, or sediment chlorophyll *a* were detected.

Intertidal *Zostera japonica* has been reported to be an annual in Washington and British Columbia (Harrison 1979, Thom 1990), but plants were present throughout the year in Yaquina Bay (Fig. 4). Mean annual above-ground *Z. japonica* biomass at the 8 locations monitored ranged from 15 to 42 g AFDW m<sup>-2</sup>. Mean annual below-ground biomass ranged from 14 to 60 g AFDW m<sup>-2</sup>. A seasonal cycle is evident in above-ground biomass, with maximum levels in late summer and early fall, and minimum levels in early spring (Fig. 4). Seasonal patterns were not evident in below-ground or total biomass (data not shown).

Table 7. Expt 3. Sediment properties in *Zostera japonica* and *Z. marina* habitats. Values are means  $\pm$  1 SD, n = 9 for all variables

Variable	Species	
	<i>Z. japonica</i>	<i>Z. marina</i>
Mean grain size (mm)	0.71 $\pm$ 0.10	0.55 $\pm$ 0.12
Grain size heterogeneity (mm)	1.17 $\pm$ 0.12	1.03 $\pm$ 0.06
POC (% dry wt)	1.43 $\pm$ 0.61	1.71 $\pm$ 0.81
PN (% dry wt)	0.10 $\pm$ 0.04	0.12 $\pm$ 0.05
PP (% dry w)	0.002 $\pm$ 0.0002	0.002 $\pm$ 0.0004
Porewater NO <sub>3</sub> ( $\mu$ M)	0.88 $\pm$ 0.75	0.75 $\pm$ 0.82
Porewater NH <sub>4</sub> ( $\mu$ M)	66.13 $\pm$ 21.51	33.82 $\pm$ 14.57
Porewater DRP ( $\mu$ M)	0.22 $\pm$ 0.11	0.28 $\pm$ 0.27



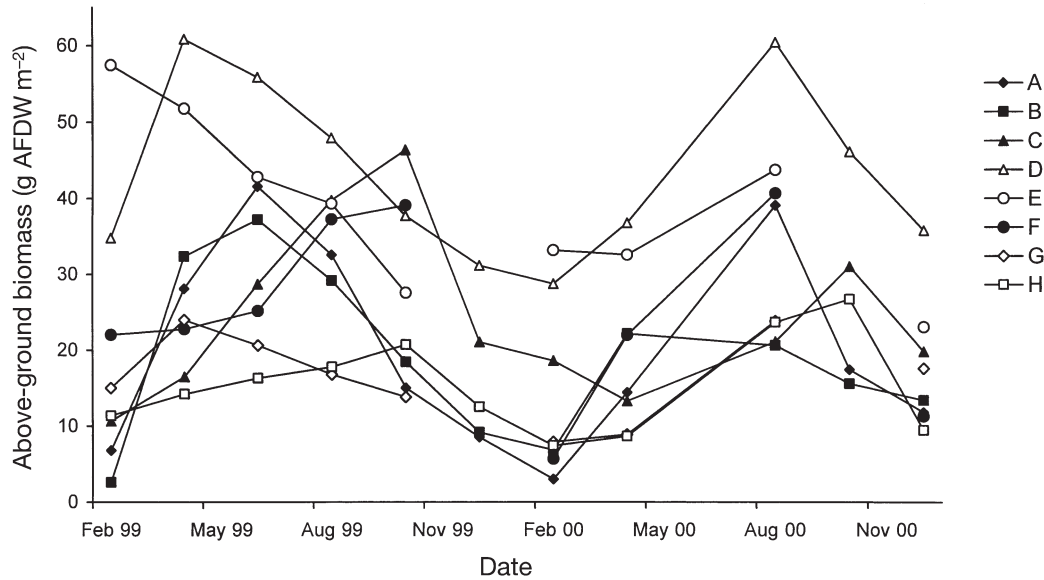


Fig. 4. *Zostera japonica*. Above-ground biomass in Yaquina Bay. Letters in key: locations on Fig. 1. Data points are means of 10 samples at Location F, 11 samples at Locations E and G, and 12 samples at the remaining locations. AFDW: ash-free dry wt

## DISCUSSION

Dissolved nutrient fluxes between the water column, and benthos represent the balance between processes that remove nutrients from the water column such as biotic assimilation, and processes that release nutrients, such as organic matter remineralization and excretion (Hemminga et al. 1991, Cowan et al. 1996, Risgaard-Petersen et al. 1998). *Zostera japonica* can shift this balance in the upper intertidal sediments it colonizes. Unvegetated sediments in Yaquina Bay were a source of  $\text{NH}_4$  to the water column in both the warm and cool season, with little net flux of  $\text{NO}_3$  or DRP. When *Z. japonica* occupied the same zone, the benthos was a net sink for  $\text{NO}_3$  and DRP in both seasons, and a sink for  $\text{NH}_4$  in the warm season.

In NE Pacific estuaries that have been invaded by *Zostera japonica*, alterations in nutrient fluxes may increase over time as biomass accumulates in new and expanding patches. Established *Z. japonica* patches in Yaquina Bay did not appear to increase in biomass during my 22 mo study (Fig. 4), but new patches appeared in spring in previously unvegetated sediment (own pers. obs.). Continued monitoring is required to assess long-term changes in *Z. japonica* biomass. Seagrass patches that are not expanding may still be long-term sinks for dissolved nutrients. Nutrient leaching from living and senescent seagrass tissues is generally orders of magnitude slower than uptake by live tissue (Buchsbaum et al. 1991, Enríquez et al. 1993), and nutrient losses in the form of detritus generally exceed dissolved nutrient losses in temperate seagrass beds (Bach et al. 1986, Pedersen & Borum 1993).

At the time of the study (1999 and 2000), *Zostera japonica* occupied between 1 and 5% of the intertidal area of the marine and mesohaline zones of Yaquina Bay, based on image-analysis of digitized airphotos (P. Clinton pers. comm.). More accurate measurements of *Z. japonica* cover are not yet available, so estimates of the estuary-wide effects of *Z. japonica* are rough. Conservative estimates of estuary-wide effects were made by assuming a percent cover value of 1% ( $\sim 24 \times 10^4 \text{ m}^2$  of the  $24 \text{ km}^2$  intertidal area) and using nutrient flux rates averaged across the study locations. *Z. japonica* habitats are estimated to remove  $50$  to  $60 \text{ mol DIN h}^{-1}$  and  $0.2$  to  $2.2 \text{ mol DRP h}^{-1}$  from the Yaquina Bay water column during the day (Table 8). Estimated rates of estuary-wide diel influx to *Z. japonica* habitats, made only for the warm season when both day and night fluxes were measured, are  $1595 \text{ mol DIN d}^{-1}$  ( $1324 \text{ mol NO}_3 \text{ d}^{-1}$  and  $271 \text{ mol NH}_4 \text{ d}^{-1}$ ), and  $31 \text{ mol DRP d}^{-1}$ . If *Z. japonica* cover in Yaquina Bay increases to the point that the marine-mesohaline area within the *Z. japonica* tidal range ( $\sim 8 \times 10^6 \text{ m}^2$ ) is entirely occupied, effects on

Table 8. Estimated estuary-wide nutrient flux rates in *Zostera japonica* habitat ( $\text{mol h}^{-1}$ ). Estimates are products of measured flux rates and conservative estimate of intertidal area of Yaquina Bay covered by *Z. japonica* ( $24 \times 10^4 \text{ m}^2$ )

Period/season	Hourly flux rate		
	$\text{NO}_3$	$\text{NH}_4$	DRP
Daylight/cool	-48.9	-6.0	-0.9
Daylight/warm	-49.6	-14.6	-2.2
Night/warm	-43.6	-9.7	-0.2

nutrient fluxes could be quite severe. In this worst-case scenario, estimated diel influx rates due to *Z. japonica* are 44 090 mol NO<sub>3</sub> d<sup>-1</sup>, 9024 mol NH<sub>4</sub> d<sup>-1</sup>, and 1032 mol DRP d<sup>-1</sup>.

The conversion of intertidal sediments from net sources of inorganic nutrients to net sinks following an invasion of *Zostera japonica* may affect pelagic productivity. DIN and DRP efflux has been shown to supply most of the nitrogen and phosphorus required for phytoplankton growth in other shallow estuaries (Rizzo 1990, Reay et al. 1995, Cowan et al. 1996). Estuarine phytoplankton may become nutrient-limited following the establishment of nonindigenous seagrasses due to reduced benthic efflux. Even in the absence of seagrasses, phytoplankton in seasonally river-dominated estuaries such as Yaquina Bay may be limited by low nutrient input during low-flow seasons (Schemel et al. 1984, Mortazavi et al. 2000). Rates of NH<sub>4</sub> and DRP influx to *Z. japonica* habitats in Yaquina Bay were highest during the summer low-flow season, indicating that reductions in benthic nutrient supplies to the water column coincided with reductions in river supplies.

Increased NH<sub>4</sub> influx, reduced NH<sub>4</sub> efflux, and shifts from NH<sub>4</sub> efflux to influx have been observed during light periods in seagrass habitats and in sediments with abundant benthic microalgae (Rizzo et al. 1992, Thornton et al. 1999, Hansen et al. 2000). These changes were attributed to light-dependent NH<sub>4</sub> assimilation. NH<sub>4</sub> influx to *Z. japonica* habitats was positively correlated with irradiance, and was significantly higher during the day than at night, consistent with previous studies. In contrast, NH<sub>4</sub> efflux from unvegetated sediments increased during the day, rather than decreasing. This result was unexpected, because benthic microalgae were abundant in unvegetated sediments, as indicated by high sediment chlorophyll *a* concentrations (Table 4).

Unlike NH<sub>4</sub> flux rates, NO<sub>3</sub> flux rates in *Zostera japonica* habitats were not strongly affected by light. These results were also unexpected, as several benthic chamber studies of subtidal *Zostera* spp. habitats have reported higher rates of NO<sub>3</sub> influx in light than in darkness (Risgaard-Petersen et al. 1998, Asmus et al. 2000, Hansen et al. 2000). Rizzo et al. (1992) attributed a lack of light-dependent NO<sub>3</sub> influx in estuarine sediments to high water-column NH<sub>4</sub> concentrations and repression of NO<sub>3</sub> uptake by NH<sub>4</sub>. In the present study, water column NO<sub>3</sub> concentrations were 3 to 17× higher than NH<sub>4</sub> concentrations, and NO<sub>3</sub> influx rates to *Z. japonica* habitats were ~5× higher than NH<sub>4</sub> influx rates, which suggests that there was little NO<sub>3</sub> repression. Rapid NO<sub>3</sub> influx at night suggests that the autotrophs in *Z. japonica* habitats maintain high levels of reducing power generated during the day. Welsh et

al. (2000) suggested that dark nutrient uptake in intertidal seagrasses represents an adaptation to decoupled light and nutrient availability in estuaries with semi-diurnal tidal regimes, such as Yaquina Bay. Water column nutrients are unavailable during daylight low tides in these estuaries, and intertidal seagrasses must store photosynthetic reducing power to assimilate nutrients during the following high tide, when light may not be available.

The rapid growth of *Zostera japonica* patches in NE Pacific estuaries (Harrison & Bigley 1982) raises the possibility that this species can outcompete and replace the native *Z. marina*, further altering nutrient source-sink patterns in the intertidal zone. Results from experimental and observational studies at a site where *Z. marina* and *Z. japonica* overlap suggested that *Z. marina* is competitively dominant, although unequivocal evidence is lacking (Nomme & Harrison 1991a,b). During the warm season in Yaquina Bay, intertidal *Z. marina* habitat was a larger DIN sink than *Z. japonica* habitat on an area-specific basis; DIN influx in *Z. marina* habitat (270 μmol m<sup>-2</sup> h<sup>-1</sup>) was nearly twice that in the *Z. japonica* habitat (144 μmol m<sup>-2</sup> h<sup>-1</sup>). This difference was probably related to differences in biomass, as the above-ground biomass of intertidal *Z. marina* was almost 3× higher than that of *Z. japonica*. *Z. japonica* had a higher mean NO<sub>3</sub> influx rate per unit above-ground biomass than *Z. marina* (Table 3), and if biomass levels of *Z. japonica* increase in the future, they may be accompanied by increased NO<sub>3</sub> influx.

Porewater DIN concentrations in the root zone of *Zostera japonica* habitats were low compared with the same depth in unvegetated sediments (Table 4). Similar patterns have been observed in some seagrass systems (Short 1983, Caffrey & Kemp 1990), while other studies have reported higher porewater NH<sub>4</sub> concentrations in seagrass habitats (Kenworthy et al. 1982). Reduced porewater DIN in seagrass habitats has been attributed to uptake by roots and rhizomes at rates higher than regeneration rates (Short 1983, Short et al. 1993). This hypothesis is supported by the results of field studies in which porewater DIN increased following seagrass removal, decreased following seagrass colonization of unvegetated sediment, and decreased further as seagrass biomass increased (Short 1983, Short et al. 1993). The results of the present study add some circumstantial evidence to the hypothesis. The mean porewater NH<sub>4</sub> concentration in *Z. japonica* habitats was twice that in *Z. marina* habitats (Table 7), a difference that may reflect higher rates of sediment nitrogen uptake in *Z. marina* habitats with greater biomass.

The establishment of *Zostera japonica* clearly alters patterns of the water column-benthos nutrient flux in

the Yaquina Bay intertidal zone. These changes appear to be the direct effects of *Z. japonica* leaves and shoots, and not indirect effects of altered sediment properties. This interpretation is supported by the significant linear regressions relating NO<sub>3</sub> influx to above-ground *Z. japonica* biomass (Table 3) and the lack of significant correlations between nutrient flux in *Z. japonica* habitats and sediment properties.

**Acknowledgements.** Many thanks to W. Dengal, P. Eldridge, M. Gobershock, C. Mohlmann, G. Sullivan, and J. Thompson for assistance in the field, and to the staff of Dynamac Corporation for assistance with sediment analyses. D. Specht kindly provided sediment temperature data, and P. Clinton provided areal coverage data for Yaquina Bay. Reviews by D. Bulthuis, J. Kaldy, R. Thom and 2 anonymous reviewers improved the manuscript. The research reported in this manuscript has been funded wholly by the US Environmental Protection Agency. The manuscript has been subjected to the Agency's peer and administrative review and has been approved for publication as an EPA document. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

#### LITERATURE CITED

- Asmus RM, Sprung M, Asmus H (2000) Nutrient fluxes in intertidal communities of a South European lagoon (Ria Formosa)—similarities and differences with a northern Wadden Sea bay (Sylt-Rømø Bay). *Hydrobiologia* 436: 217–235
- Bach SD, Thayer GW, LaCroix, MW (1986) Export of detritus from eelgrass (*Zostera marina*) beds near Beaufort, North Carolina, USA. *Mar Ecol Prog Ser* 28:265–278
- Buchanan JB (1984) Sediment analysis. In: Holme NA, McIntyre AD (eds) *Methods for the study of marine benthos*. IBP Handbook 16, 2nd edn. Blackwell Scientific Publishers, Boston, p 41–65
- Buchsbaum R, Valiela I, Swain T, Dzierzeski M, Allen S (1991) Available and refractory nitrogen in detritus of coastal vascular plants and macroalgae. *Mar Ecol Prog Ser* 72: 131–143
- Caffrey JM, Kemp WM (1990) Nitrogen cycling in sediments with estuarine populations of *Potamogeton perfoliatus* and *Zostera marina*. *Mar Ecol Prog Ser* 66:147–160
- Cohen AN, Carlton, JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–557
- Cowan JLW, Pennock JR, Boynton WR (1996) Seasonal and interannual patterns of sediment-water nutrient and oxygen fluxes in Mobile Bay, Alabama (USA): regulating factors and ecological significance. *Mar Ecol Prog Ser* 141: 229–245
- Eno NC (1996) Non-native marine species in British waters: effects and controls. *Aquat Conserv Mar Freshw Ecosys* 6:215–228
- Enriquez S, Duarte CM, Sand-Jensen K (1993) Patterns in decomposition rates among photosynthetic organisms: the importance of detritus C:N:P content. *Oecologia* 94: 457–471
- Forja JM, Gomez-Parra A (1998) Measuring nutrient fluxes across the sediment-water interface using benthic chambers. *Mar Ecol Prog Ser* 164:95–105
- Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecol Appl* 8:975–989
- Hansen J, Pedersen AU, Berntsen J, Ronbog IS, Hansen LS, Lomstein BA (2000) Photosynthesis, respiration and nitrogen uptake by different compartments of a *Zostera marina* community. *Aquat Bot* 66:281–295
- Harrison PG (1979) Reproductive strategies in intertidal populations of two co-occurring seagrasses (*Zostera* spp.). *Can J Bot* 57:2635–2638
- Harrison PG, Bigley RE (1982) The recent introduction of the seagrass *Zostera japonica* Aschers. and Graebn. to the Pacific coast of North America. *Can J Fish Aquat Sci* 39: 1642–1648
- Hemminga MA, Harrison PG, van Lent F (1991) The balance of nutrient losses and gains in seagrass meadows. *Mar Ecol Prog Ser* 71:85–96
- Hemminga MA, Koutstaal BP, van Soelen J, Merks AJA (1994) The nitrogen supply to intertidal eelgrass (*Zostera marina*). *Mar Biol* 118:223–227
- Kenworthy WJ, Zieman JC, Thayer GW (1982) Evidence for the influence of seagrasses on the benthic nitrogen cycle in a coastal plain estuary near Beaufort, North Carolina (USA). *Oecologia* 54:152–158
- Meyerson LA, Chambers RM, Vogt KA (1999) The effects of *Phragmites* removal on nutrient pools in a freshwater tidal marsh ecosystem. *Biol Invasions* 1:129–136
- Mortazavi B, Iverson RL, Landing WM, Lewis FG, Huang W (2000) Control of phytoplankton production and biomass in a river-dominated estuary: Apalachicola Bay, Florida, USA. *Mar Ecol Prog Ser* 198:19–31
- Nomme KM, Harrison PG (1991a) A multivariate comparison of the seagrasses *Zostera marina* and *Zostera japonica* in monospecific versus mixed populations. *Can J Bot* 69: 1984–1990
- Nomme KM, Harrison PG (1991b) Evidence for interaction between the seagrasses *Zostera marina* and *Zostera japonica* on the Pacific coast of Canada. *Can J Bot* 69: 2004–2010
- Pedersen MF, Borum J (1993) An annual nitrogen budget for a seagrass *Zostera marina* population. *Mar Ecol Prog Ser* 101:169–177
- Pérez-Lloréns JL, de Visscher P, Nienhuis PH, Niell FX (1993) Light-dependent uptake, translocation and foliar release of phosphorus by the intertidal seagrass *Zostera noltii* Hornem. *J Exp Mar Biol Ecol* 166:165–174
- Posey MH (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69:974–983
- Posey MH, Wigand C, Stevenson JC (1993) Effects of an introduced aquatic plant, *Hydrilla verticillata*, on benthic communities in the upper Chesapeake Bay. *Estuar Coast Shelf Sci* 37:539–555
- Reay WG, Gallagher DL, Simmons GM (1995) Sediment-water column oxygen and nutrient fluxes in nearshore environments of the lower Delmarva Peninsula, USA. *Mar Ecol Prog Ser* 118:215–227
- Risgaard-Petersen N, Dalsgaard T, Rysgaard S, Christensen PB, Borum J, McGlathery K, Nielsen LP (1998) Nitrogen balance of a temperate eelgrass *Zostera marina* bed. *Mar Ecol Prog Ser* 174:281–291
- Rizzo WM (1990) Nutrient exchanges between the water column and a subtidal benthic microalgal community. *Estuaries* 13:219
- Rizzo WM, Lackey GJ, Christian RR (1992) Significance of euphotic, subtidal sediments to oxygen and nutrient cycling in a temperate estuary. *Mar Ecol Prog Ser* 86: 51–61

- Rooth SE, Stevenson JC (2000) Sediment deposition patterns in *Phragmites australis* communities: implications for coastal areas threatened by rising sea-level. *Wetlands Ecol Manage* 8:173–183
- Ruiz GM, Fofonoff P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. *Limnol Oceanogr* 44:950–972
- Schemel LE, Harmon DD, Hager SW, Peterson DH (1984) Response of northern San Francisco Bay to riverine inputs of dissolved inorganic carbon, silicon, nitrogen and phosphorus. In: Kennedy VS (ed) *The estuary as a filter*. Academic Press, New York, p 221–240
- Short FT (1983) The response of interstitial ammonium in eelgrass (*Zostera marina* L.) beds to environmental perturbations. *J Exp Mar Biol Ecol* 68:195–208
- Short FT, Montgomery J, Zimmermann CF, Short CA (1993) Production and nutrient dynamics of a *Syringodium filiforme* Kütz: seagrass bed in Indian River Lagoon, Florida. *Estuaries* 16:323–334
- Templer P, Findlay S, Wigand C (1998) Sediment chemistry associated with native and non-native emergent macrophytes of a Hudson River marsh ecosystem. *Wetlands* 18:70–78
- Thom RM (1990) Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Bot Mar* 33:497–510
- Thornton DCO, Underwood GJC, Nedwell DB (1999) Effect of illumination and emersion period on the exchange of ammonium across the estuarine sediment-water interface. *Mar Ecol Prog Ser* 184:11–20
- Turner CE, Center TD, Burrows DW, Buckingham GR (1998) Ecology and management of *Melaleuca quinquenervia*, an invader of wetlands in Florida, USA. *Wetlands Ecol Manage* 5:165–178
- Welsh DT, Bartoli M, Nizzoli D, Castadelli G, Riou SA, Viaroli P (2000) Denitrification, nitrogen fixation, community primary productivity and inorganic-N and oxygen fluxes in an intertidal *Zostera noltii* meadow. *Mar Ecol Prog Ser* 208:65–77

*Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA*

*Submitted: April 3, 2002; Accepted: December 5, 2002  
Proofs received from author(s): May 12, 2003*