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Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia

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ABSTRACT: The exotic seagrass *Zostera japonica* was first documented on the Pacific Coast of North America in the late 1950s, and has extensively colonized formerly unvegetated tidal flats and dramatically altered the habitat structure. In Boundary Bay, British Columbia, Canada, there was an almost 17-fold increase in *Z. japonica* coverage between 1970 and 1991. In Boundary Bay's 6385 ha of intertidal and shallow subtidal area (tidal range 4.7 m), *Z. japonica* occurred mostly from 0 to -1.8 m Mean Water Level (MWL) and covered 3845 ha in October 1991 The native *Z. marina* occurred mostly from −0.9 to −5.5 m MWL, and covered 3444 ha including 1684 ha of overlap with *Z. japonica*. Standing stock of *Z. japonica*, mostly in formerly unvegetated areas, measured 520 metric tonnes (t) above ground and 235 t below ground in October 1991 This introduced species provides an important feeding habitat for many migratory waterfowl. Percent dry mass of *Z. japonica* in esophagus contents of birds collected in Boundary Bay was 57.2% (n = 62) in brant *Branta bernicla*, 84.8% (n = 45) in American wigeon *Anas americana*, 72.3% (n = 20) in mallard *A. platyrhynchos*, 48.3% (n = 54) in northern pintail *A. acuta*, and 1.7% (n = 14) in green-winged teal *A. crecca*. Percent dry mass of the native *Z. marina* was 41.2% in esophagi of brant but only 0.1 to 4.6% in the other species. Grazing by brant and dabbling ducks, with peak numbers of about 80000 in early December, removed 50% (262 t) of the above-ground biomass and 43% (100 t) of the below-ground biomass of *Z. japonica*. This exotic seagrass thereby supported almost 4.6 million use days by these birds.

KEY WORDS: *Zostera japonica* · *Zostera marina* · Exotic · Grazing · Seagrass · Waterfowl

INTRODUCTION

Biological invasions have significantly changed many aquatic ecosystems, often adversely, e.g. spread of the submerged plant *Myriophyllum spicatum* in Chesapeake Bay, USA (Bayley et al. 1978), zebra mussels *Dreissena polymorpha* in the Great Lakes (Hebert et al. 1991), and the emergent grass *Spartina alterniflora* in San Francisco Bay, California, USA (Callaway & Josselyn 1992). Effects of many other introductions are difficult to characterize. For example, about 100 exotic invertebrates have become established in San Francisco Bay, but their presence was not realized for nearly 100 years (Nichols & Pamatmat 1988).

Zostera japonica was probably introduced to the north Pacific Coast of North America in the first half of this century along with oyster shipments from Japan. It was first documented in 1957 in Willapa Bay, Washington, USA, and in Boundary Bay, British Columbia, Canada, in 1969 (Fig. 1) (Harrison & Bigley 1982). Since then *Z. japonica* has spread throughout Boundary Bay, northern Puget Sound, and the southern Strait of Georgia, as well as to coastal bays in Oregon, USA.

Zostera japonica has many characteristics of a successful invader. It has small body size (leaves usually < 20 cm long and 2 mm wide) and devotes up to 25% of its dry mass per unit area to flowering and seed production (Den Hartog 1970, Harrison 1979). *Z. japonica*'s main reproductive strategy is to germinate in spring in mid to low intertidal zones that have been denuded by weather and storm waves in winter, and to produce many seeds before storms again uproot its shallow below-ground system in late autumn (Harrison 1982a). In contrast, the native *Z. marina* has a larger body size, with leaves often 50 to 120 cm long and 3 to 12 mm wide. In this north Pacific region, *Z. marina* devotes a large fraction of its resources to rhizomes and shoots for over-wintering and vegetative reproduction, and flowers comparatively little beginning only in its second year (Harrison 1979). (See Jacobs 1982 for contrasting strategies in Europe.) *Z. marina* overwinters at low intertidal to subtidal elevations, where exposure to storm waves and weather are reduced. Penetration to higher elevations by *Z. marina* appears limited by its lower resistance to desiccation, whereas at lower elevations the greater leaf growth of *Z. marina*, when continuously submerged under summer irradiance, may shade out *Z. japonica* (Harrison 1982b). Although some competition occurs between the 2 species, *Z. japonica* probably will not displace *Z. marina* (Harrison 1982b, Nomme 1989). Many bays in this north Pacific region were easily invaded by *Z. japonica*, because of an unoccupied niche and a physical and climatic similarity to the species' original habitat (Den Hartog 1970, Mukai et al. 1980).

Grazing of seagrasses and submerged aquatic vegetation (SAV) by waterfowl has been well documented (Cottam et al. 1944, Campbell 1946, Yocom & Keller 1961, Ogilvie & Matthews 1969, Grandy 1972, Charman 1977, 1979, Tubbs & Tubbs 1983, Phillips 1984, Thayer et al. 1984, Mayhew 1988), and some workers have estimated the biomass removed (Ranwell & Downing 1959, McRoy 1966, Stieglitz 1966, Anderson & Low 1976, Cornelius 1977, Nienhuis & Van Ierland 1978, Kiorboe 1980, Verhoeven 1980, Jacobs et al. 1981, Wilkins 1982, Ward 1983, Nienhuis & Groenendijk 1986, Mitchell 1991). However, there is almost no published information on waterfowl use of *Zostera japonica*. Thom et al. (1991) estimated the mass of carbon of *Z. marina* and *Z. japonica* removed by brant *Branta bernicla*, American wigeon *Anas americana*, mallard *A. platyrhynchos*, northern pintail *A. acuta* and green-winged teal *A. crecca* in Padilla Bay, Washington (Fig. 1); however, they lacked data on the fraction of either *Zostera* species in bird diets.

In this study we document the dramatic spread of *Zostera japonica* in Boundary Bay, its contribution to waterfowl diets, and its biomass grazed by waterfowl.

MATERIALS AND METHODS

Study area. Boundary Bay, SW British Columbia, Canada, is delimited partly by the USA-Canada border (Fig. 1). Boundary Bay is in the Fraser River Delta, but fresher water from the Fraser River probably never enters the Bay. Boundary Bay is freshened slightly on the east end by 2 small rivers, but salinity throughout most of the Bay remains near levels in the Strait of

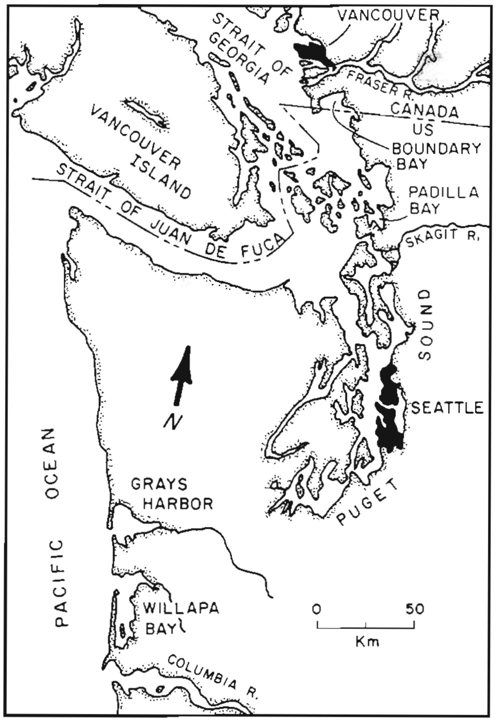

Fig. 1. Southwest British Columbia, Canada, and western Washington, USA

Georgia (24 to 29‰) (Waldichuk 1957). A mixed semidiurnal tide (2 high and 2 low tides each lunar day) over a 4.7 m elevational range results in extensive tidal flats. Tide references in this paper are to Mean Water Level (MWL = Geodetic Datum) and Lower Low Water (LLW = Chart Datum); see Forrester (1983) for explanation of tide terminology.

***Zostera* distribution and standing stock.** Three 200 m transects were established in a monotypic stand of *Zostera japonica* in 1990–91 and 1991–92 in western Boundary Bay. Transects were 50 to 75 m apart, each with 20 stations at 10 m intervals marked with stakes. Percent cover within a 0.1 m^2 (20 × 50 cm) rectangular frame was visually estimated at each station in October 1990 and September 1991 before most ducks arrived, and again in January 1991 and December 1991 after ducks had reached peak numbers.

Core samples were taken along 2 additional transects in early October, December and February in both years. Transects extended perpendicular to the shoreline from the edge of the salt marsh at 72nd Street (Transect 1) and 96th Street (Transect 2) (see Fig. 3). Sampling stations were marked with stakes at 100 m intervals. Three cores per station were taken during each sampling period with a hand-held, galvanized-steel sampler (20 cm diameter) to a depth of 5 to 6 cm. Samples were washed over a 0.5 mm screen and both leaves and rhizomes were sorted to species. Samples were oven-dried at 50 °C and weighed.

Transect stations were surveyed for elevation using a stadia rod and level. Bench marks used as reference are relative to MWL or mean exposure time. Distributions of *Zostera* spp. relative to elevations along these transects were extrapolated to the entire Bay based on the bathymetric map of Kellerhals & Murray (1969). The lower elevational limit of *Z. marina* was about –5.5 m MWL (S. D. Freeman pers. comm.). Areal coverages of salt marsh, unvegetated sandflat, *Z. japonica*, mixed *Zostera* spp., and *Z. marina* were determined from maps (based on aerial photographs) with a Lasico electronic compensating polar planimeter. Above-ground and below-ground biomass were estimated from core samples taken along both transects in October 1991. Triplicate samples were pooled within stations and then averaged to estimate dry mass m^{-2}. Mean biomass and areal coverage were used to calculate the biomass of *Z. japonica* leaves and rhizomes for the entire Bay. Areal coverage of *Zostera* spp. in 1970 was mapped from aerial photographs and verified by site inspection (British Columbia Dept of Wildlife, Burnaby, unpubl. data).

Waterfowl numbers. Numbers of American wigeon, northern pintail, mallard and green-winged teal were estimated every 7 to 10 d from September through March 1990–91 and 1991–92. Duck numbers were estimated with a spotting scope from points on the dike along the northern edge of the bay. Daylight, tide height, wind and fog dictated when estimates were possible. Daily 'waterfowl use days' (*WUD*) were calculated from averages of consecutive counts and summed for each species. No data for brant numbers were available, so use days were estimated by assuming that 500 brant were present for 20 d. Total use days were used to calculate the biomass of *Zostera japonica* eaten by waterfowl from September to March (see below).

Foraging behavior. Foraging behavior of wigeon, pintails and mallards was observed from 1 October through 7 December 1990. Daylight hours were divided into 4 equal parts, and ducks were observed for 2 non-consecutive 30 min periods, once a week, during each of the 4 daylight periods. Tide heights during observations ranged from ca –1.1 to +2.1 m MWL. A focal bird (Altmann 1974) was randomly selected and observed for 20 s (n = 1153 focal individuals). Duck behavior was recorded on cassette tapes, later transcribed, and the percent time spent feeding determined for 6 tide height ranges. These data were not normally distributed, so medians and 15 to 85 % quantiles were used to delimit about the same fraction of the distribution as ± 1 standard deviation (68 %).

Esophagus contents. Wigeon, pintail, mallard and green-winged teal were collected in Boundary Bay from October through January 1990–91 and 1991–92. Birds were collected during the day with a shotgun at most tidal ranges, although the lowest tides occur at night during winter in this area. Brant esophagi were obtained from hunters along the southwest shoreline of the Bay from 1 to 10 March 1992.

Esophagus contents were either immediately preserved in ethyl alcohol or frozen. Food items were sorted to species, oven-dried at 50 °C, and weighed to the nearest mg. Percent dry mass of each food item was calculated for each esophagus sample, and aggregate percentages (Swanson et al. 1974) were calculated for the major food groups of each species.

Eelgrass energy content. Samples of *Zostera* spp. were collected once a month from September to March. Leaves were washed to remove epiphytes, and all samples were freeze-dried to constant weight and ground to pass a 0.1 mm screen. A Phillipson micro-bomb calorimeter was used to estimate the gross energy in *Zostera* spp. leaves and rhizomes, and the seeds of *Z. japonica*. These estimates were used in calculating the biomass consumed by waterfowl (see below).

Biomass of eelgrass removed. Consumption of *Zostera japonica* leaves, rhizomes and seeds was estimated for wigeon, pintail, mallard and brant for both years. Biomass removed (*BR*) by wigeon, pintail, mallard and brant was calculated by the following formula applied to each species:

$$BR = [(DM \times DEE) / (\text{kJ g}^{-1}{}_{l,r,s} \times AME)] \times WUD.$$

DM is the average fraction of esophagus contents (dry mass) made up of *Z. japonica* for a given species. Estimates of daily energy expenditure (*DEE*) were 631 kJ d^{-1} for wigeon (Mayhew 1988), 683 kJ d^{-1} for mallard (Morton et al. 1989), 660 kJ d^{-1} for pintail (interpolated for a body mass of 900 g from values for wigeon and mallard) and 842 kJ d^{-1} for brant (Drent et al. 1978/79). We measured gross energies of *Z. japonica* leaves, rhizomes and seeds (kJ $g^{-1}{}_{l,r,s}$) with micro-bomb calorimetry. We used literature values for apparent metabolizable energy (*AME*) of leaves (46 %; Buchsbaum et al. 1986), rhizomes (56 %; McRoy 1970, Karasov 1990) and seeds (59 %; Karasov 1990). Waterfowl use days were estimated as described above.

RESULTS

Zostera distribution and standing stock

Percent cover of *Zostera japonica* decreased from early fall to midwinter by an average of 88 % the first year and 91 % the second year (Table 1). In the first

Table 1. *Zostera japonica*. Mean (SD) percent cover of eelgrass in Boundary Bay, British Columbia, during early fall and midwinter: October 1990 vs January 1991 (n = 60 stations), and September vs December 1991 (n = 40 stations)

Year	Transect	% Cover Early fall	% Cover Midwinter	% Loss
1990-91	1	17.3 (13.7)	2.2 (1.1)	87.3 (11.9)
	2	10.7 (10.6)	1.2 (1.4)	89.2 (8.2)
	3	6.0 (4.0)	0.7 (0.4)	88.2 (10.7)
1991	1	56.4 (23.5)	4.1 (2.7)	92.5 (4.0)
	2	64.0 (21.8)	6.0 (4.1)	90.4 (6.4)

year, ice cover in mid-December (see Fig. 4) delayed the midwinter sample until January. In the second year, markers along one transect disappeared after the first sampling period, which prevented resampling.

Transect 1 was steeper and dropped sharply to below LLW, about −2.6 m MWL, at 2.2 km from the edge of the salt marsh (Fig. 2). Transect 2 did not drop below LLW until about 4 km from the edge of the saltmarsh, but was not sampled beyond 2.6 km because of poor drainage and insufficiently low tides during winter sampling periods. *Zostera japonica* occurred in shallow pools above MWL, but its distribution generally began near MWL and extended to around −1.8 m MWL. *Z. marina* occurred mostly below −0.9 m MWL. These elevational ranges are somewhat lower than reported for other sites in the region (e.g. Posey 1988, Thom 1990), probably because Boundary Bay has sandy sediments that drain faster and more completely, a steady elevational gradient (no persistent tide pools) and greater exposure to waves.

In 1970, about 211 ha of *Zostera japonica* were established in Boundary Bay (Fig. 3A). By 1991, coverage of *Z. japonica* had increased over 17-fold to 3845 ha (Fig. 3B). *Z. marina* coverage increased 121% from 1560 ha in July 1970 to 3444 ha in October 1991. In October 1991, total eelgrass coverage was 5605 ha, with 1684 ha of overlap of the 2 *Zostera* species (Table 2). Based on the average biomass m^{-2} from pooled transect samples, the above-ground standing stock for 3845 ha of *Z. japonica* in October 1991 was 520 t (95% CI = 399 to 641) and the below-ground biomass (rhizomes) was 235 t (95% CI = 182 to 288).

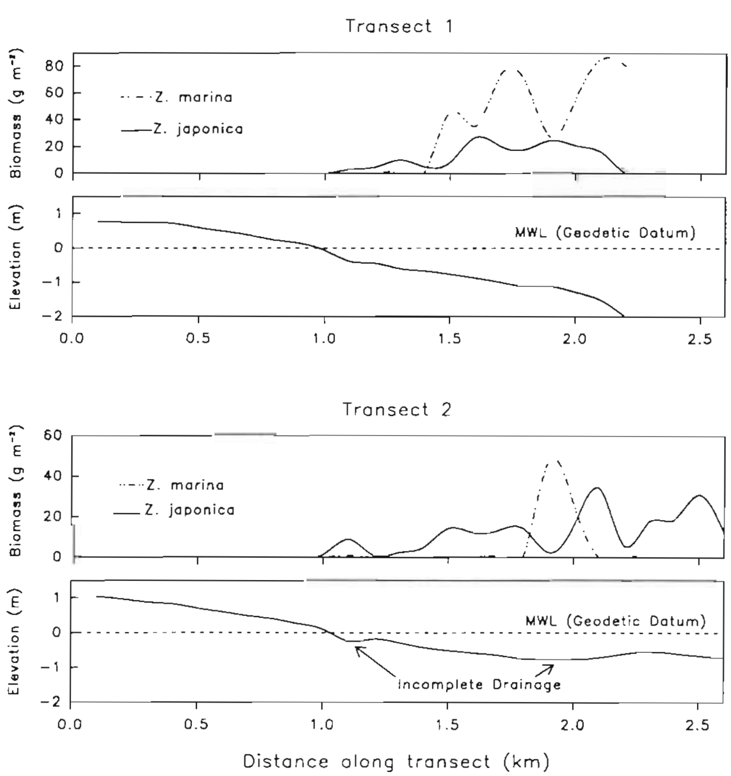

Fig. 2. *Zostera marina, Z. japonica*. Biomass of eelgrass in Boundary Bay, British Columbia, relative to Mean Water Level (MWL) and to distance along transects extending from the edge of the salt marsh perpendicular to the shoreline

Duck numbers

Duck numbers climbed steadily in Boundary Bay from September through November in both years (Fig. 4). Numbers peaked at about 80000 in early December and then declined, probably depending on weather conditions and food availability. In some winters such as 1990–91, extensive freeze-ups encourage ducks to continue migration or disperse from the area (authors' unpubl. data).

Foraging behavior and diet

Below MWL, wigeon, pintails and mallards spent most of their time feeding, whereas almost no time was spent feeding above MWL (Table 3). This abrupt elevational change in feeding effort corresponded to the upper limit of *Zostera japonica* (Fig. 2).

Zostera japonica comprised the largest percentage of the diet for all species except green-winged teal (Table 4). Leaves of *Z. japonica* were the single largest fraction of the diet for brant and wigeon, whereas the rhizomes of *Z. japonica* were the largest fraction for pintails and mallards. *Z. marina* was a

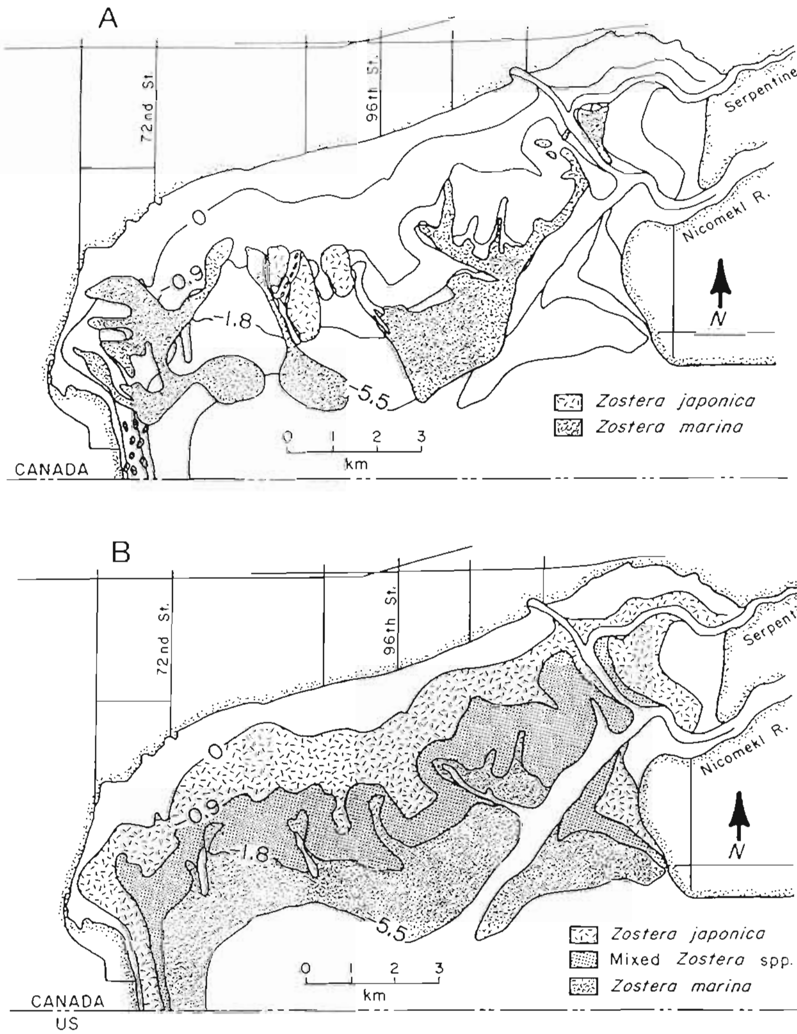

Fig. 3. *Zostera* spp. Estimated eelgrass distribution in Boundary Bay, British Columbia, (A) in July 1970 (Environment Canada unpubl. data) and (B) in October 1991. Transects for eelgrass sampling extended from the edge of the saltmarsh perpendicular to shoreline at 72nd Street (Transect 1, 2.2 km long) and 96th Street (Transect 2, 2.6 km long)

large portion of the brant diet (41.2%), but had little importance (0.1 to 4.6%) to the other species. *Ulva* sp. is usually found only as drift in Boundary Bay and comprised only 5.8 and 1.6% of the diet for wigeon and brant respectively. *Ruppia maritima*, which occurs throughout the bay but only in small patches, was seldom eaten.

Table 2. Area of different cover types in Boundary Bay, British Columbia, in October 1991 (see also Fig. 3B)

Flooding regime	Cover type	Area (ha)
Infrequently flooded	Saltmarsh	182
High intertidal	Unvegetated sandflats	598
Mid intertidal	*Zostera japonica*	
	Above *Z. marina* zone	2161
	Mixed with *Z. marina*[a]	1684
	Total	3845
Low intertidal/ subtidal	*Zostera marina*	
	Mixed with *Z. japonica*[a]	1684
	Below *Z. japonica* zone	1760
	Total	3444

[a]Area of mixed *Zostera* species is included in the total for each species

Energy content and biomass removed

Mean energy content (kJ g^{-1}) for *Zostera marina* was 16.817 (SE = 0.345, n = 23) for leaves and 15.713 (SE = 0.247, n = 14) for rhizomes (no seeds were analyzed). For *Z. japonica*, values were 18.145 (SE = 0.260, n = 19) for leaves, 15.387 (SE = 0.640, n = 6) for rhizomes and 18.999 (SE = 0.183, n = 2 aggregate samples) for seeds. Leaves of *Z. japonica* had a higher energy content than leaves of *Z. marina* (*t*-test; $p < 0.005$), but there was no difference between the rhizomes (*t*-test; $p = 0.61$).

Dabbling ducks and brant consumed an estimated 362.4 t of *Zostera japonica* leaves and rhizomes in

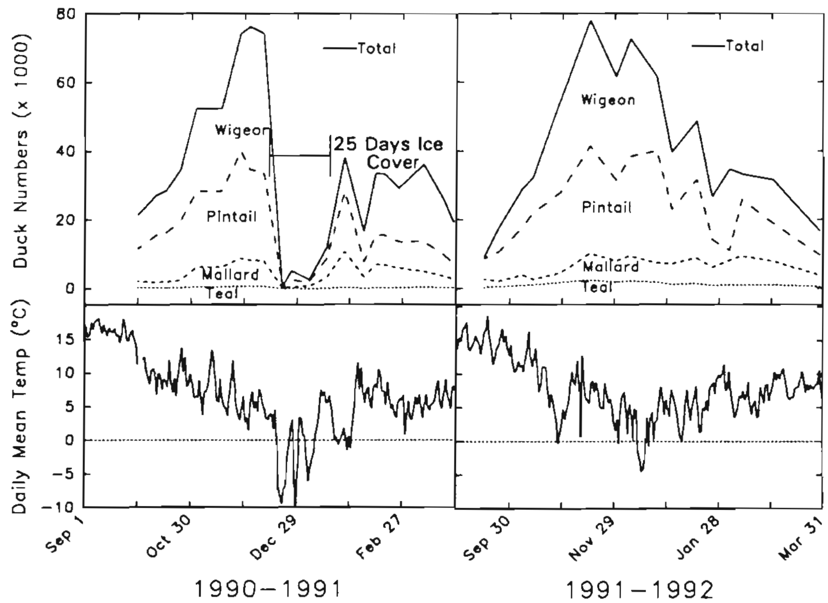

Fig. 4. *Anas americana, A. acuta, A. platyrhynchos, A. crecca.* Numbers of American wigeon, northern pintail, mallard and green-winged teal in Boundary Bay, British Columbia, in the winters of 1990-91 and 1991-92, and daily mean air temperatures from Vancouver International Airport (18 km northwest of Boundary Bay)

1991-92 (Table 5), which was 50.5% of the aboveground standing stock of 520 t and 42.5% of the belowground biomass of 235 t (see above).

DISCUSSION

In the last 25 yr, *Zostera japonica* has spread rapidly in Boundary Bay and the Puget Sound/Strait of Georgia region. Harrison & Bigley (1982) documented its distribution from Coos Bay, Oregon, to Vancouver, British Columbia, with large beds occurring in Willapa Bay, Grays Harbor and Padilla Bay (Fig. 1). As of 1990, *Z. japonica* was not found in southern Puget Sound (Thom & Hallum 1990) or in many isolated bays in the Strait of Georgia, but may eventually colonize all suitable habitat in the Pacific Northwest. In Boundary Bay, growth of *Z. japonica* in the middle to upper intertidal zone has added 2161 ha of seagrass habitat, millions of bird use days, and hundreds of metric tonnes of organic matter. Sediment organic matter content of only 1.3% (authors' unpubl. data) indicates that this large biomass of eelgrass detritus does not decompose *in situ* (cf. Hemminga & Niewenhuize 1991), but rather decomposes in large heaps windrowed along shorelines (Koop & Lucas 1983) or else is exported to deeper water.

Based on their energy requirements, waterfowl removed about 50% of the above-ground stock of *Zostera japonica* from September to March. This value is within the range reported for avian grazers in other seagrass systems by Ranwell & Downing (1959; 30 to 75%), Kiorboe (1980; 34 to 67%), Jacobs et al. (1981; 51%) and Mitchell (1991; 74%), and somewhat higher than that obtained by McRoy (1966; 17%), Stieglitz (1966; 32%), Anderson & Low (1976; 40%), Cornelius (1977; 21%), Nienhuis & Van Ierland (1978; 1.5% of NPP May to August), Wilkins (1982; 25%) and Ward (1983; 31%). In addition to grazing impacts, mallards and pintails often accessed rhizomes by digging and enlarging pits in the sediment, similarly to waterfowl digging for *Scirpus robustus* rhizomes in North Carolina (Smith 1983) and for *Z. noltii* shoots and rhizomes in the Netherlands (Jacobs et al. 1981). Smith (1980) concluded that 18 to 31% of intertidal sediments in nearby Skagit Bay (Fig. 1) could be recovering from this type of waterfowl disturbance at a given time.

Effects of *Zostera japonica* on other fauna have been addressed in only a few studies. Posey (1988) documented an overall increase in macroinvertebrate diversity and abundance with spread of *Z. japonica*. However, the tubeworm *Praxillella gracilis* and the ghost shrimp *Neotrypaea californiensis*, which burrow mostly in unvegetated sandflats, apparently avoid areas colonized by *Z. japonica* with its obstructing root system and perhaps greater predator densities (Harrison 1987). In nearby Padilla Bay (Fig 1), where some *Z. japonica* persists through winter owing to less exposure to storm waves, Thom et al. (1991) found that numbers of grazing isopods (mostly *Idotea resecata*) and gastropods (*Lacuna variegata*) per m^2 of quadrat

Table 3. *Anas americana, A. acuta, A. platyrhynchos.* Medians and 15-85% quantiles (in parentheses) for percent time spent feeding at different tide heights (MWL) in Boundary Bay, British Columbia, 1 October to 7 December 1990. For medians without ranges there was no variation. Sample sizes refer to the number of 20 s, focal-individual samples

Tide height (m)	American wigeon (n = 472)	Northern pintail (n = 386)	Mallard (n = 295)
-1.1 to -0.6	100	100	100 (0-100)
-0.6 to -0.3	100	100	75 (0-100)
-0.3 to 0.0	25 (0-100)	100 (65-100)	80 (0-100)
0.0 to 0.3	0 (0-100)	0 (0-100)	0 (0-100)
0.3 to 0.6	0 (0-100)	0 (0-30)	0
0.6 to 2.1	0	0	0

Table 4. *Anas americana, A. acuta, A. platyrhynchos, Branta bernicla*. Esophagus contents (% dry mass) of birds collected in Boundary Bay, British Columbia, October to March 1990–92

Food	American wigeon (n = 45)	Northern pintail (n = 54)	Mallard (n = 20)	Green-winged teal (n = 14)	Brant (n = 62)
Zostera japonica					
Seeds	–	15.8	13.4	0.8	–
Leaves	84.0	8.2	19.9	0.9	57.2
Rhizomes	0.8	24.3	39.0	–	–
Zostera marina					
Seeds	–	0.6	Trace[b]	0.1	–
Leaves	2.7	3.0	4.6	–	41.2
Rhizomes	–	Trace	–	–	Trace
Ulva spp.	5.8	–	–	–	1.6
Ruppia maritima	1.0	0.2	Trace	Trace	–
Other[a]	5.7	47.9	23.0	98.2	–

[a]Includes gastropods, amphipods, isopods, decapods, bivalves, oligochaetes, insects, and seeds of *Salicornia, Distichlis, Chenopodium*, and *Suaeda* (Baldwin & Lovvorn 1992)
[b]Trace represented < 0.1% dry mass

Table 5. *Anas americana, A. acuta, A. platyrhynchos, Branta bernicla*. Use days and *Zostera japonica* consumption by 4 species of waterfowl in Boundary Bay, British Columbia, September to March 1990–91 and 1991–92

Species	Use days	*Z. japonica* consumed (t)		
		Leaves	Rhizomes	Seeds
1990–91				
Wigeon	3 252 653	159.4	1.5	–
Pintail	2 510 817	16.3	46.7	23.4
Mallard	850 829	13.9	26.3	6.9
Brant[a]	10 000	0.6	–	–
Total	6 624 295	190.2	74.5	30.3
1991–92				
Wigeon	3 541 339	221.9	2.0	–
Pintail	3 496 011	22.7	65.1	32.5
Mallard	1 061 046	17.3	32.8	8.7
Brant[a]	10 000	0.6	–	–
Total	8 198 396	262.5	99.9	41.2

[a]Brant use days were estimated; no counts were available

samples were higher in *Z. japonica* than in *Z. marina* throughout their study period of October to July. The grazing amphipod *Caprella laeviuscula* was more numerous in *Z. japonica* in May to July. Numerical densities of decapods, gammarid amphipods, cumaceans and a variety of other invertebrates are also higher in *Z. japonica* than on unvegetated tidal flats (Dinnel et al. 1986, Simenstad et al. 1988, authors' unpubl. data). These invertebrates are important foods of both fish and waterbirds in this region (Vermeer & Levings 1977, MacDonald 1984, Simenstad et al. 1988, Thom et al. 1991, authors' unpubl. data).

The dominant paradigm for most seagrass ecosystems is that detrital pathways, as opposed to grazing, are the main routes to animal production (Kikuchi 1980, Simenstad 1983, Phillips 1984). This is thought to be especially true in temperate areas where there are few large herbivores as compared to the tropics (Ogden & Lobel 1978, McRoy & Helfferich 1980, McRoy & Lloyd 1981, Zieman 1982). In tropical areas, large herbivores include manatees, fish, turtles and birds, whereas birds are the only large herbivores in temperate seagrass systems. However, the role of birds should not be minimized. Phillips (1984) listed 19 species of birds in the Pacific Northwest of North America which consume some portion of eelgrass, and underestimated the role of the numerous mallard and pintail by presuming they eat only seeds. Our results and others cited above (e.g. Ranwell & Downing 1959, Kiorboe 1980, Jacobs et al. 1981), suggest that the trophic role of avian herbivores in temperate seagrass food webs may often be underemphasized.

Although *Zostera japonica* was introduced inadvertently, it may be an unusual example of an exotic species being generally beneficial to major components of an ecosystem. *Z. japonica* is now a principal food of migrating and wintering waterfowl in the Fraser Delta and other important sites such as Padilla Bay (Fig. 1). *Z. japonica* is also adding many metric tonnes of organic matter to the detrital system (Simenstad 1983), and birds grazing *Z. japonica* might bypass the slow decomposition process by excreting several tonnes of fecal nitrogen (cf. Thayer et al. 1982). For example, based on the estimated fecal output of European wigeon *Anas penelsope* of 65.2 g dry mass bird^{-1} d^{-1} (Mayhew 1988), American wigeon alone excrete 221 t of feces into Boundary Bay in 7 mo. Greater consumption of the exotic *Z. japonica* than of native *Z. marina* by ducks and brant (Table 4) might result primarily from *Z. japonica*'s longer accessibility during the daily tidal cycle (authors' unpubl. data). However, this diet pattern might also be influenced by the higher energy content of *Z. japonica*'s leaves and easier handling of its smaller vegetative parts (Summers & Atkins 1991).

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