

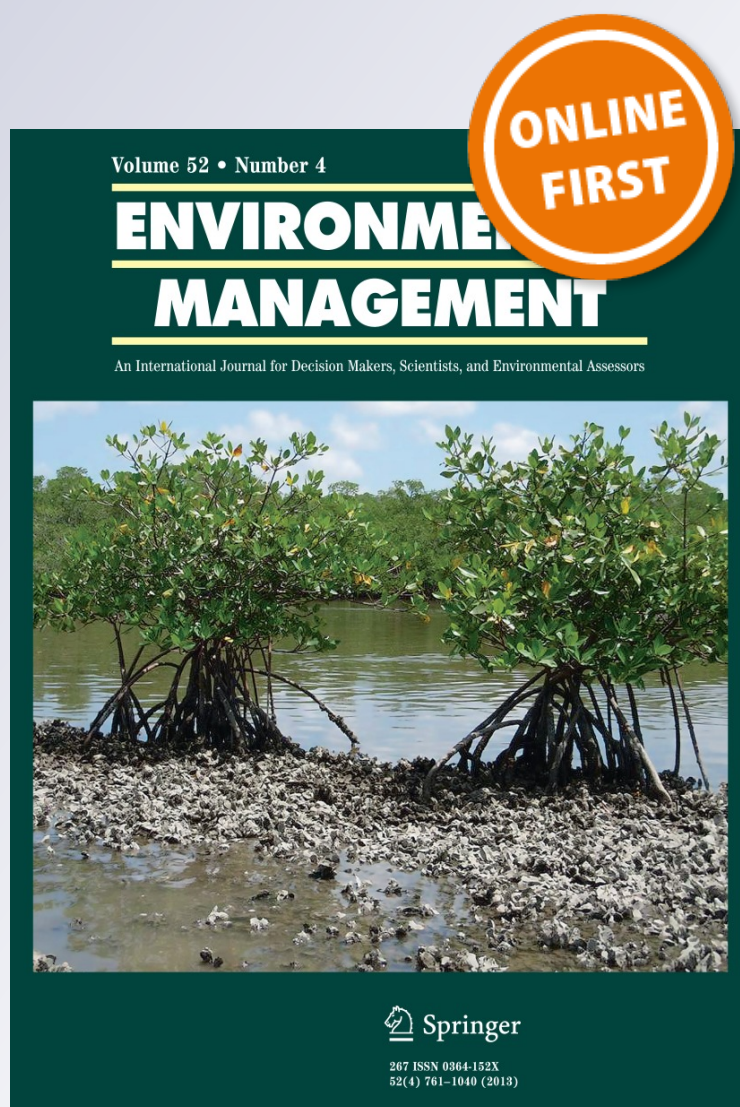
# *Science and Management of the Introduced Seagrass *Zostera japonica* in North America*

**Deborah J. Shafer, James E. Kaldy & Jeffrey L. Gaeckle**

**Environmental Management**

ISSN 0364-152X

Environmental Management  
DOI 10.1007/s00267-013-0172-z



**Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media New York (outside the USA). This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Science and Management of the Introduced Seagrass *Zostera japonica* in North America

Deborah J. Shafer · James E. Kaldy ·  
Jeffrey L. Gaeckle

Received: 7 January 2013 / Accepted: 13 September 2013  
© Springer Science+Business Media New York (outside the USA) 2013

**Abstract** Healthy seagrass is considered a prime indicator of estuarine ecosystem function. On the Pacific coast of North America, at least two congeners of *Zostera* occur: native *Zostera marina*, and introduced, *Zostera japonica*. *Z. japonica* is considered “invasive” and therefore, ecologically and economically harmful by some, while others consider it benign or perhaps beneficial. *Z. japonica* does not appear on the Federal or the Oregon invasive species or noxious weed lists. However, the State of California lists it as both an invasive and noxious weed; Washington State recently listed it as a noxious weed. We describe the management dynamics in North America with respect to these congener species and highlight the science and policies behind these decisions. In recent years, management strategies at the state level have ranged from historical protection of *Z. japonica* as a priority habitat in Washington to eradication in California. Oregon and British Columbia, Canada appear to have no specific policies with regard to *Z. japonica*. This fractured management approach contradicts efforts to conserve and protect seagrass in other regions of the US and around the world. Science must play a critical role in the assessment of *Z. japonica* ecology and

the immediate and long-term effects of management actions. The information and recommendations provided here can serve as a basis for providing scientific data in order to develop better informed management decisions and aid in defining a uniform management strategy for *Z. japonica*.

**Keywords** Seagrass · *Zostera japonica* · *Zostera marina* · Invasive species management

## Background

Seagrass habitat provides a wide variety of important ecosystem services (Orth et al. 2006a; Fourqurean et al. 2012). Major threats to seagrass include declining water quality often associated with coastal zone development that leads to a global decrease in the extent of seagrass beds and an intense interest to protect, conserve and restore seagrass beds worldwide (Short and Wyllie-Echeverria 1996; Orth et al. 2006a; Waycott et al. 2009). Although there are over 60 species of seagrass globally, only *Zostera japonica* Ascher. & Graeb and *Halophila stipulacea* (Forssk.) Ascher., are considered to be “invasive” (Williams 2007; Willette and Ambrose 2009).

Despite a few attempts to adopt a standardized terminology, the terms ‘invasive,’ ‘non-indigenous,’ ‘introduced,’ ‘exotic,’ ‘alien,’ ‘naturalized,’ and ‘non-native’ are often used interchangeably or inconsistently leading to a great deal of confusion (Colautti and MacIsaac 2004; Occhipinti-Ambrogi and Galil 2004). United States Executive Order 13112 defined ‘invasive species’ as “an alien species whose introduction does or is likely to cause economic or environmental harm or harm to human health” (Beck et al. 2008). To be considered *invasive* in this context, it is

---

D. J. Shafer  
Engineer Research and Development Center, US Army Corps of  
Engineers, 3909 Halls Ferry Rd, Vicksburg, MS 39180, USA

J. E. Kaldy (✉)  
Western Ecology Division, US EPA, 2111 SE Marine Science  
Dr, Newport, OR 97365, USA  
e-mail: Kaldy.jim@epa.gov

J. L. Gaeckle  
Aquatics Division, Washington State Department of Natural  
Resources, Nearshore Habitat Program, 1111 Washington Street  
SE, Olympia, WA 98504, USA

assumed that the negative effects associated with the organism's presence overshadow any beneficial effects. However, differing societal values and management goals influence perceptions of the relative harm or benefit associated with a particular organism. Perspectives may also change as additional data are acquired, or as a result of changing human values or management goals (Invasive Species Advisory Committee 2006). Inconsistent and imprecise terminology can lead to divergent interpretations and confusion of issues and ideas (Colautti and MacIsaac 2004), making it difficult for managers to develop appropriate responses (Stocker 2004). Although some non-indigenous species may cause severe economic and ecological damage, 80–90 % have few demonstrated effects (Williamson 1996). Positive interactions of introduced species are being increasingly recognized (Wonham et al. 2005; Thomsen 2010).

On the Pacific coast of North America, at least two seagrass congeners in the genus *Zostera* occur: native *Zostera marina* L., and *Z. japonica*. In the Pacific Northwest the distribution of the native *Z. marina* appears to be relatively stable, with some localized losses (Gaekle et al. 2011). In contrast, over the last 3–5 decades there has been a large increase in the distribution of *Z. japonica* (Posey 1988; Baldwin and Lovvorn 1994a; Young et al. 2008; Gaekle et al. 2011). Successful introduction, colonization, and expansion of *Z. japonica* has resulted in development of new habitat types that coastal managers must integrate into existing management plans. This shift from unstructured mudflat to a vegetated habitat has ecological effects; the valuation of those effects is the center of the debate and management actions. Depending on the location and stakeholder group in North America, *Z. japonica* may be perceived as a harmful invader, a benign introduced species, or a species that provides positive habitat benefits, which has led to inconsistent management practices (Table 1).

Our purpose is to review the existing science on the biology and ecology of *Z. japonica*, to review management actions with respect to *Z. japonica*, and to recommend additional science that may inform managers as they develop and plan strategies for *Z. japonica* habitat. In addition, we identify a number of critical information gaps that need to be addressed in order to understand the long-term consequences of management actions related to the presence of the introduced seagrass *Z. japonica* in North America. Throughout this document, we will refer to *Z. japonica* as “introduced” rather than “invasive,” because a group of seagrass scientists recently concluded that there was insufficient science to determine the relative economic or environmental harm associated with the presence of this seagrass (Mach et al. 2010).

## Biology and Ecology of *Zostera japonica*

### Introduction of *Zostera japonica* to North America

Aquaculture has long been recognized as a vector for introductions of non-native species both as pests and as commercial products (Quayle 1964). *Z. japonica* was first collected in Washington State in 1957 (Hitchcock et al. 1969), and is thought to have been introduced early in the twentieth century along with oyster stock imported from Japan (Harrison and Bigley 1982). Imported oysters may have been packed in seagrass to prevent desiccation during shipment (Harrison 1976). The first large-scale introductions of Pacific oysters (*Crassostrea gigas*) from Japan to Samish Bay in Puget Sound began in 1919 and continued for decades thereafter (Lindsay and Simons 1997). Japanese oysters were imported to Willapa Bay, Washington, in 1928 and their initial success led to increased oyster imports in subsequent years (Sayce 1976). Although importation of oyster seed stock continued into the 1980s (Harrison and Bigley 1982), steps were taken in the early 1950s to prevent accidental introduction of other organisms (Quayle 1953). Consequently, the first introductions of *Z. japonica* likely occurred early in the twentieth century, when large shipments were transported with minimal precautions (Harrison and Bigley 1982). Genetic comparison will be required to determine the origin of *Z. japonica* populations in North America.

### Distribution and Zonation Patterns

Within its native range, *Z. japonica* has an extremely broad latitudinal distribution, encompassing subtropical and temperate climates from southern Vietnam (~10°N latitude) to Kamchatka, Russia (~50°N latitude) (Green and Short 2003; Fig. 1). Native latitudinal distribution of herbaceous plants tends to be a good predictor of potential distribution as introduced species (Rejmanek 1995), suggesting that *Z. japonica* in North America could eventually range from Canada to Costa Rica. Assuming a 6 km year<sup>-1</sup> southward migration (Shanks et al. 2003), *Z. japonica* could colonize San Francisco Bay by 2080.

For the last few decades, North American populations of *Z. japonica* were limited to bays and estuaries in British Columbia (Canada), and Washington, Oregon and northern California (USA) (Fig. 2). Within this range, dramatic expansions have occurred in some areas, creating large beds that occupy many hectares of intertidal flats in Boundary Bay, British Columbia, and in Padilla, Samish, and Willapa Bays, Washington (Posey 1988; Baldwin and Lovvorn 1994a, b; Bulthuis 1995; Dumbauld and

**Table 1** Classification of *Zostera japonica* by various Federal and State agencies within its established range in the United States

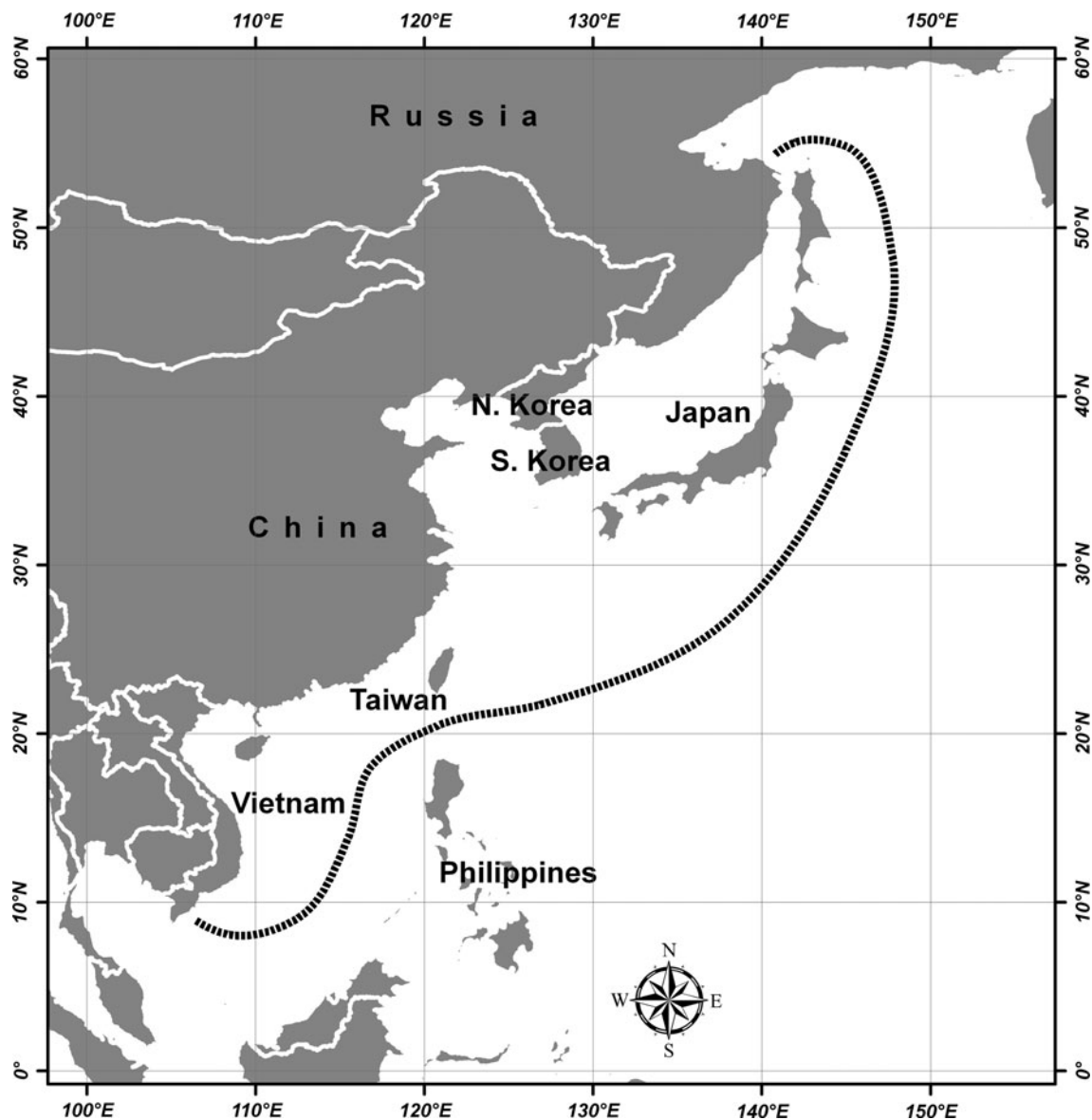
Agency	<i>Zostera japonica</i> classification	Reference
Federal Noxious Weed List	Not listed	<a href="http://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/weedlist.pdf">http://www.aphis.usda.gov/plant_health/plant_pest_info/weeds/downloads/weedlist.pdf</a> . Accessed 25 April 2012 <a href="http://plants.usda.gov/java/noxiousDriver#introduced">http://plants.usda.gov/java/noxiousDriver#introduced</a> <a href="http://www.invasivespeciesinfo.gov/">http://www.invasivespeciesinfo.gov/</a>
Federal Invasive Species list	Not listed	
California Dept Food Agriculture	Noxious weed rating “Q.” Economic or environmental detriment, but whose status is uncertain because of incomplete identification or inadequate information	<a href="http://www.cdfa.ca.gov/plant/ipc/weedinfo/winfo_list-synonyms.htm">http://www.cdfa.ca.gov/plant/ipc/weedinfo/winfo_list-synonyms.htm</a> . Accessed 10 August 2012 <a href="http://www.cdfa.ca.gov/plant/ipc/encycloweedia/encycloweedia_hp.htm">http://www.cdfa.ca.gov/plant/ipc/encycloweedia/encycloweedia_hp.htm</a>
California Invasive Plant Council	Moderate-Species have substantial and apparent-but generally not severe, ecological impacts on physical processes, plant and animal communities, and vegetation structure. Reproductive biology and other attributes are conducive to moderate to high rates of dispersal, though establishment is generally dependent on ecological disturbance Ecological amplitude and distribution may range from limited to widespread	<a href="http://www.cal-ipc.org/ip/inventory/index.php#inventory">http://www.cal-ipc.org/ip/inventory/index.php#inventory</a> . Accessed 18 April 2012
Washington State Noxious Weed Control Board	Class C Noxious Weed limited to commercially managed shellfish beds only. Washington State Department of Ecology Aquatic Pesticide Permits Program is currently considering National Pollution Discharge Elimination System (NPDES) and State Waste Discharge permits for application of the aquatic herbicide imazamox to control <i>Z. japonica</i> on shellfish beds	<a href="http://www.nwcb.wa.gov/searchResults.asp?class=C">http://www.nwcb.wa.gov/searchResults.asp?class=C</a> . Accessed 14 Dec 2012
	Washington Noxious Weed Control Board. Designated Class C listing throughout State. Adoption of Permanent Rules Amendments to WAC 16-750 for 2013. 11 Dec. 2012	<a href="http://www.nwcb.wa.gov/siteFiles/WSNWCB%20CES%202013.pdf">http://www.nwcb.wa.gov/siteFiles/WSNWCB%20CES%202013.pdf</a> . Accessed 17 December 2012
Oregon Dept. of Fish and Wildlife	Not listed	<a href="http://cms.oregon.gov/ODA/PLANT/WEEDS/docs/weed_policy.pdf">http://cms.oregon.gov/ODA/PLANT/WEEDS/docs/weed_policy.pdf</a> . Accessed 10 August 2012

Wyllie-Echeverria 2003). Recently, Young et al. (2008) determined that *Z. japonica* distribution in Yaquina Bay, Oregon, increased from 3.7 ha in 1998 to almost 19 ha in 2007, roughly a 400 % increase over 9 years.

Several researchers have suggested that this species has only colonized a small fraction of the available suitable habitat throughout its potential range in North America (Harrison and Bigley 1982; Shafer et al. 2008, 2011). In British Columbia, *Z. japonica* has been observed on the west and east coasts of Vancouver Island, Johnstone Strait, and the Strait of Georgia (Gillespie 2007). *Z. japonica* is common throughout Puget Sound (Gaeckle et al. 2011). An informal survey conducted during 1999 and 2000 identified *Z. japonica* in the Columbia River, Nehalem, Netarts, Tillamook, Salmon River, Siletz Bay, Yaquina and Coquille embayments along the Oregon coast (S. Larned, unpublished data). The Coos, Nestucca, and Umpqua Bay systems in Oregon also have *Z. japonica* populations (Lee and Brown 2009). In 2002, a small population was discovered in Humboldt Bay, California, representing a southerly range extension; in 2006 a second population was discovered nearby (Dean et al. 2008).

In its native range, *Z. japonica* has been reported to grow as deep as 3–7 m (datum not specified), although it typically grows at depths <1 m (Hayashida 2000; Nakaoka and Aoi 2001; Abe et al. 2010). Throughout its established range in North America, *Z. japonica* is found primarily in mid- to upper-intertidal zones, and has not been observed growing subtidally (Harrison 1982a; Thom 1990; Bulthuis 1995; Shafer 2007; Britton-Simmons et al. 2010). In Puget Sound, *Z. japonica* has been found as deep as 0 m mean lower low water (MLLW) (J. Gaeckle pers. obs.). In British Columbia and Oregon, *Z. japonica* typically occurs between +1 and +3 m MLLW (Harrison 1982b; Nomme and Harrison 1991; Kaldy 2006a). In Willapa Bay, Washington, *Z. japonica* was documented between +0.1 and +1.5 m MLLW, while *Z. marina* was only found below +0.6 m MLLW (Ruesink et al. 2010), but has been found to grow above +1 m in Puget Sound (Gaeckle et al. 2011).

Due to the depth distribution of *Z. japonica* in North America, it co-occurs with *Z. marina* in three distinct vertical zonation patterns (Fig. 3). In the disjunct zonation (Fig. 3a), the *Z. japonica* bed is separated from the *Z.*

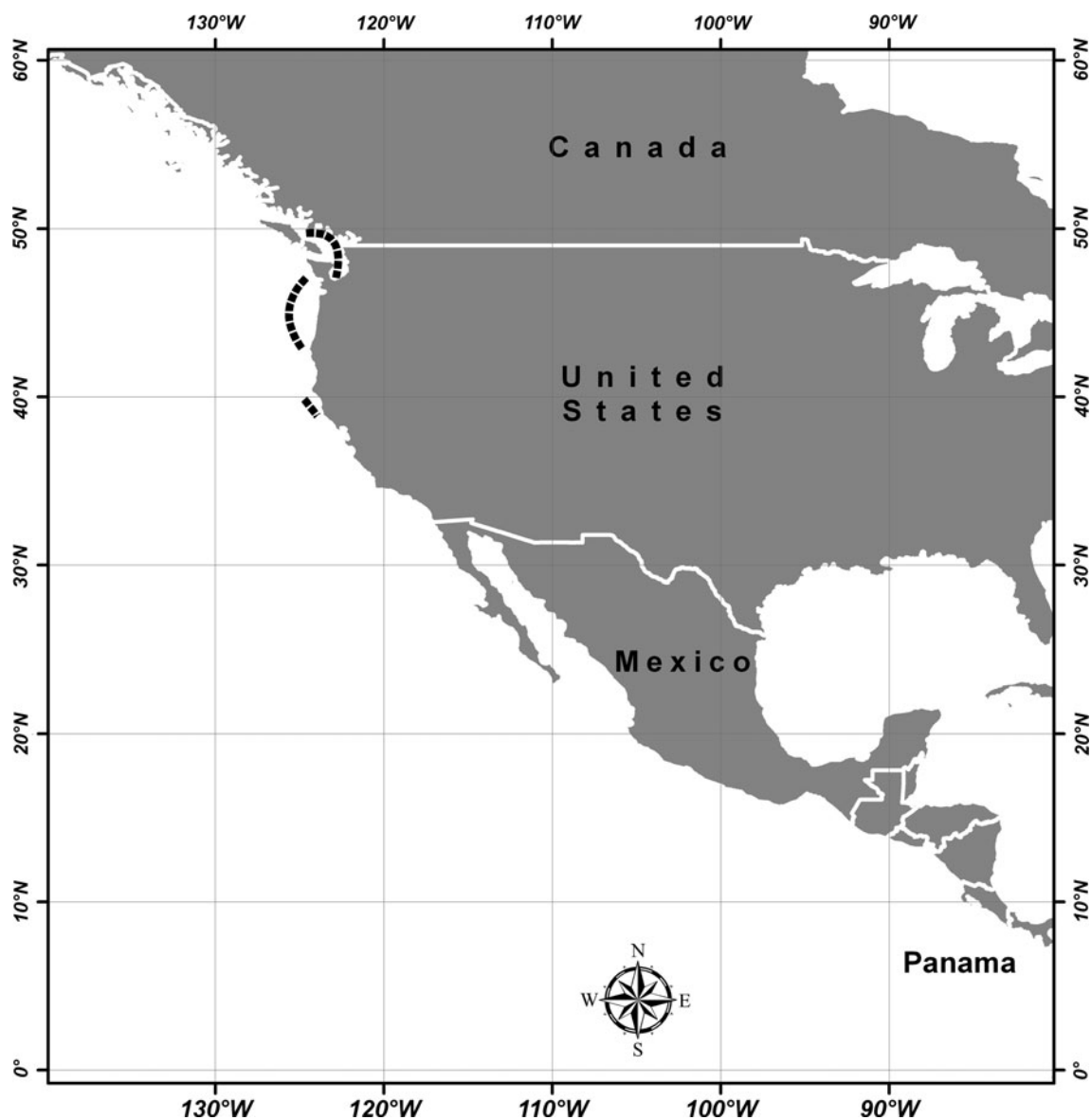


**Fig. 1** Current distribution (represented by *dashed line*) of *Zostera japonica* in its native range

*marina* bed by unvegetated sediments. These areas are characterized by a steep intertidal slope and a narrow fringing *Z. japonica* bed. The disjunct zonation pattern is the most common, occurring at 70 % of the sites surveyed (Table 2). The overlapping zonation pattern (Fig. 3b) is characterized by mixed beds or discrete patches of both species at the same intertidal elevation. Overlapping zonation was observed at sites with gently sloping topography and represented 31 % of sites surveyed (Table 2). The mosaic zonation pattern (Fig. 3c) is characterized by micro-topographic relief creating small pools with *Z. marina* interspersed with *Z. japonica* on well-drained hummocks. Mosaic sites, which often co-occur with the overlapping zonation pattern, are characterized by broad, expansive intertidal flats with very little slope (Harrison

1982a; Shafer 2007) and are generally localized in larger estuarine systems such as Boundary Bay, Padilla Bay, and Willapa Bay (Table 2).

Another factor that may influence vertical zonation of *Z. japonica* and *Z. marina* is differences in their thermal optima; *Z. japonica* in North America is warm water adapted with an optimal growth temperature of 20 °C (Lee et al. 2005; Shafer et al. 2008, 2011). In contrast, *Z. marina* is cold water adapted with an optimum temperature of between 6 and 13 °C (Phillips 1984; Thom et al. 2001). *Z. japonica* plants grown at 20 °C exhibit leaf growth rates ( $\text{mg dw sht}^{-1} \text{day}^{-1}$ ) that are five times faster than plants grown at 8 °C (Kaldy and Shafer, unpublished data). Field studies from 2002 with complete annual cycles show that *Z. japonica* growth ranges

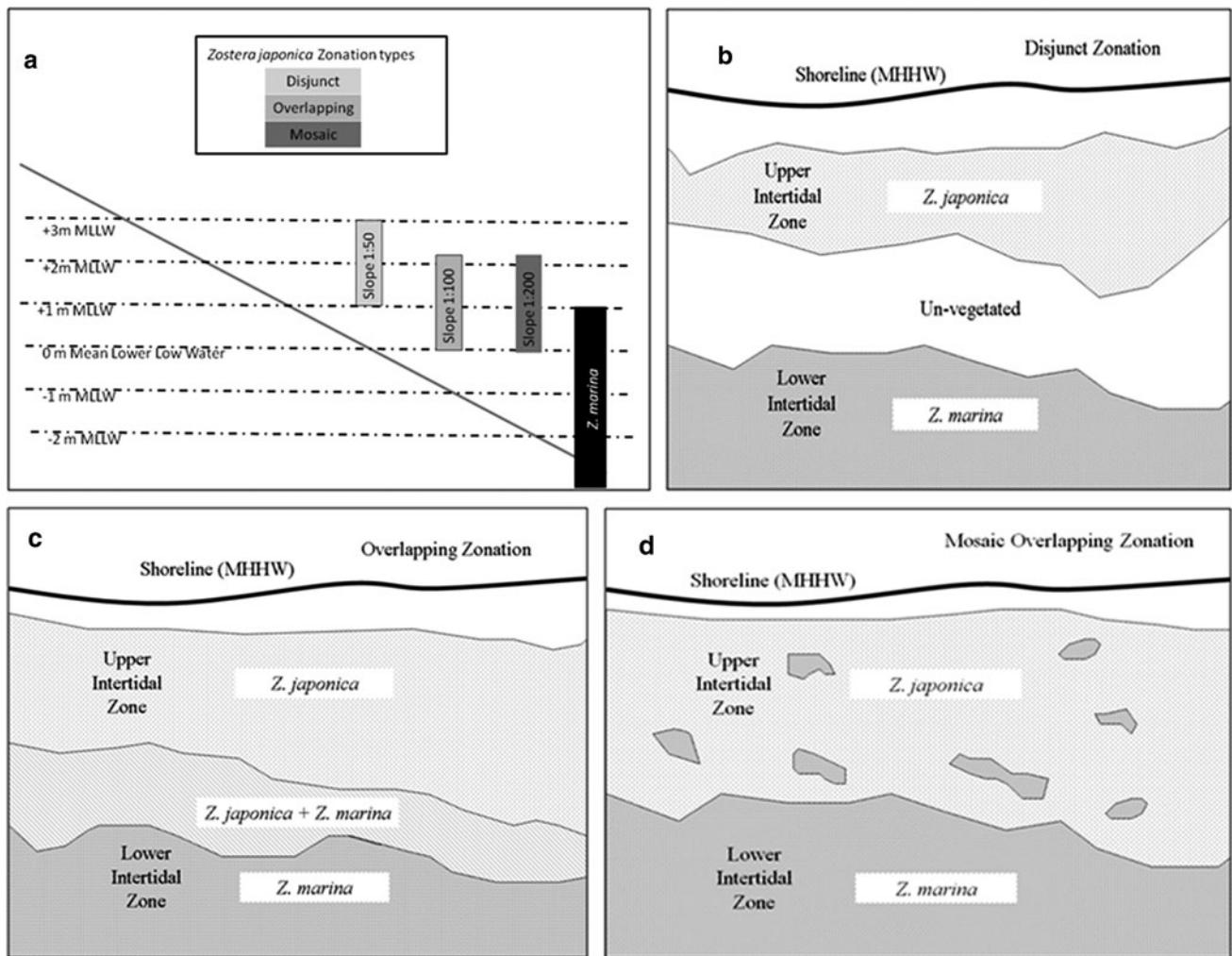


**Fig. 2** Current distribution (represented by *dashed line*) of *Zostera japonica* in North America

(summer to winter) between  $0.5$  and  $1.8 \text{ gdw m}^{-2} \text{ day}^{-1}$  (Kaldy 2006a), while *Z. marina* growth rates (summer to winter) range between  $0.4$  and  $2.2 \text{ gdw m}^{-2} \text{ day}^{-1}$  (Kaldy 2006b). These growth rates are based on ambient field conditions (e.g., water temperatures  $8\text{--}12 \text{ }^{\circ}\text{C}$ ); consequently, we would expect greater growth rates at warmer temperatures. *Z. japonica* has a lethal thermal threshold of about  $35 \text{ }^{\circ}\text{C}$  (Kaldy and Shafer 2012). Because optimum growth of *Z. japonica* occurs at temperatures that cause stress to *Z. marina*, and *Z. japonica* grows slowly at low temperatures where *Z. marina* thrives, it is possible that these differences in thermal optima may contribute to the maintenance of disjunct zonation patterns in these species (Shafer et al. 2008).

#### Life History Strategies

*Zostera japonica* exhibits morphological and life-history characteristics (e.g., high reproductive output, small size, and fast growth) that make it a successful colonizer of previously unoccupied mudflat (Ruesink et al. 2010). Near the northern limits of its range in British Columbia, *Z. japonica* is considered to be an annual or short-lived perennial and rarely over-winters; new populations are initiated each year from seed produced the previous year (Harrison 1982b). Oregon populations of *Z. japonica* are perennial, persisting throughout the year (Kaldy 2006a). Due to the lower frequency of reproductive shoots in the southern population, clonal expansion may be more



**Fig. 3** Zonation patterns of *Z. japonica* and *Z. marina* in North America. **a** Conceptual diagram of how bathymetric slope and elevation interact to form zonation patterns. *Diagonal line* represents hypothetical bathymetry, *dashed lines* represent tidal elevations

relative to mean lower low water (MLLW). Slopes are order of magnitude estimates. **b** Disjunct zonation. **c** Overlapping zonation. **d** Mosaic zonation. In panels **b** through **d**, the shoreline is delimited as mean higher high water (MHHW)

important than seed production in the maintenance of southern *Z. japonica* populations (Kaldy 2006a).

### Dispersal Mechanisms

The establishment of new seagrass populations in previously un-occupied areas or the re-colonization of disturbed areas depends on species-specific dispersal capabilities (Orth et al. 1994). Most free seagrass seeds are negatively buoyant and are unlikely to be transported more than a few meters from the parent plants (Ruckelshaus 1996; Orth et al. 2006b), leading to limited dispersal capabilities. However, there are three potential long-distance dispersal pathways that are likely to be important to *Z. japonica*: (1) transport of reproductive stems and viable seed by tidal currents and watercraft, (2) the transfer of viable fragments

that establish on unvegetated shorelines, and (3) transport of viable seeds by migratory waterfowl.

Waves, currents, and mechanical disturbance from anthropogenic activities can dislodge sections of seagrass shoots, rhizomes, and roots from the sediment; rafts of these vegetative fragments, known as wrack, can often be seen drifting on the surface. Although much of this wrack eventually decomposes and enters the detrital food web (Mateo et al. 2006), shoots containing attached roots and rhizomes may remain viable and provide a mechanism for plant dispersal (Ewanchuk and Williams 1996; Hall et al. 2006). Some studies have suggested that *Z. marina* seed transport can be on the order of 50–100 km (Reusch 2002; Harwell and Orth 2002). Transport of wrack by boats and trailers is also a possible dispersal vector. The potential capacity of vegetative dispersal has not been assessed for most seagrass species.



**Table 2** Zonation classifications of locations in Canada, Washington, Oregon, and California where *Z. japonica* and *Z. marina* co-occur. Because the overlap and mosaic distribution types sometimes intermingle, total percent occurrence can exceed 100 %

Site	Classification			Source
	Disjunct	Overlap	Mosaic	
Canada				
Roberts Bank		X		Nomme and Harrison (1991), Harrison (1987)
Boundary Bay			X	Harrison (1982a), Baldwin and Lovvorn (1994a)
Washington				
Sucia Island	X			Wyllie-Echeverria, pers. obs.
Samish Bay	X			Shafer, pers. obs.
Padilla Bay	X	X	X	Thom (1990), Bulthuis (1995), Shafer pers. obs.
Whidbey Island, Max Welton		X		Shafer, pers. obs.
Shaw Island, Indian Cove	X			Shafer, pers. obs.
Shaw Island, Picnic Cove	X			Shafer, pers. obs.
Dumas Bay	X	X		Shafer, pers. obs., Ferrier and Gaeckle 2011
Willapa Bay		X	X	Dumbauld, pers. comm., Author, pers. obs.
>70 SVMP sites throughout Puget Sound	X	X	X	Gaeckle et al. (2011)
Oregon				
Tillamook Bay	X			Yamada, pers. comm.
Netarts Bay		X		Dudoit (2006)
Yaquina Bay	X			Kaldy (2006a), Shafer, pers. obs.
Coquille Bay	X			Dudoit 2006
Coos Bay	X			Dudoit (2006), Rumrill, pers. comm.
California				
Humboldt Bay	X			Wyllie-Echeverria, pers. obs.

Another potential mechanism for spread of *Z. japonica* involves ingestion and subsequent excretion of seeds by waterfowl (Figuerola and Green 2002; Figuerola et al. 2002; Charalambidou et al. 2003). Passage through the

avian digestive tract may enhance seed germination (Figuerola et al. 2002). Several waterfowl species, including swans (*Cygnus* spp.), dabbling ducks (*Anas* spp.), coots (*Fulica atra*), black brant (*Branta bernicla*), and Canada geese (*Branta canadensis*) are known to feed heavily on *Z. marina* and *Z. japonica* seeds, leaves, and rhizomes (Baldwin and Lovvorn 1994a, b; Ganter 2000; Rivers and Short 2007). A recent study found that geese and ducks forage in *Z. japonica* habitat predominantly between August and January (Lamberson et al. 2011), which correlates directly with the peak plant reproduction (Kaldy 2006a). In addition, American coot (*Fulica americana*), wigeon (*A. americana*), northern pintail (*A. acuta*), Canada geese, and mallard were observed to directly consume *Z. japonica* (Lamberson et al. 2011). This evidence suggests that waterfowl could be a major vector in the establishment of new *Z. japonica* populations. Detailed genetic studies of multiple *Z. japonica* populations will be required to evaluate the sources of propagules, and the direction of colonization occurring at the regional scale.

## Ecosystem Effects

### Competitive Interactions with Native Seagrass

Ecological impacts associated with the establishment of invasive species in aquatic ecosystems may include competition with native species for resources, declines in native species diversity, or complete displacement of native species (Drake et al. 1989). In most Pacific Northwest systems where *Z. japonica* and *Z. marina* co-occur, the populations exhibit a disjunct distribution (Fig. 3b). Consequently, with a few notable exceptions, such as Padilla Bay and Willapa Bay, Washington, there is little opportunity for direct competition between the native and introduced *Zostera* species (Shafer 2007). Where the two species do overlap, neither species exhibits clear competitive dominance over the other; density and biomass of both species are reduced in the presence of the other (Harrison 1982a; Hahn 2003a; Bando 2006). Therefore, *Z. japonica* does not appear likely to displace existing subtidal *Z. marina* beds, nor can *Z. marina* effectively compete in the intertidal zone where *Z. japonica* is dominant (Harrison 1982b). So it is possible to have an overall increase in the amount of seagrass habitat without loss of native seagrass habitat.

In a statistical comparison of co-occurring native and introduced plant species, Daehler (2003) concluded that alien species did not generally exhibit clear advantages with respect to growth rates, competitive ability, or reproductive output. Instead, the performance of most native species was equal to or exceeded that of introduced species. Daehler (2003) concluded that the relative

performance of native and introduced species appears to be largely dependent on specific environmental conditions. This seems to be the case with *Z. marina* and *Z. japonica*, because they have different physiological characteristics and tolerances that contribute to their different zonation patterns in North America (Shafer et al. 2008, 2011).

#### Benthic Invertebrate Community Composition

Studies of the effects of *Z. japonica* on intertidal benthic invertebrate community composition have been limited; however, the existing data suggest that *Z. japonica* supports diverse benthic assemblages. Posey (1988) examined changes in benthic community composition and abundance and concluded that species diversity and abundance were greater in *Z. japonica* than in adjacent un-vegetated sediments. Benthic invertebrate community composition, abundance, species richness, and diversity associated with patches of *Z. japonica* and *Z. marina* in Washington were similar (Hahn 2003a). Recent work concluded that benthic macrofaunal species richness, abundance, and biomass in *Z. japonica* habitat was greater than or equal to that in oyster (*C. gigas*), mud shrimp (*Upogebia pugettensis*), or *Z. marina* habitat (Ferraro and Cole 2012). However, the activities of some benthic invertebrates can affect the survival and establishment of *Z. japonica*. Established populations of burrowing shrimp (*Neotrypaea californiensis*) are capable of causing complete mortality of transplanted *Z. japonica* (Harrison 1987) and preventing its natural recruitment from seed (Dumbauld and Wyllie-Echeverria 2003).

#### Biogeochemical Cycling

Seagrasses are primary producers, providing carbon to the estuarine food web and providing structural support for other primary producers (e.g., epiphytes and microphytobenthos). The largest proportion of seagrass primary production (~65 %) is decomposed within the meadow, while the remainder is either exported (~15 %), grazed (<10 %), or accumulated in a refractory pool (~10 %) (Mateo et al. 2006). *Z. japonica* decomposes much more rapidly than *Z. marina*, which could lead to more rapid nutrient cycling, and higher levels of both primary and secondary production in colonized ecosystems (Hahn 2003b). Preliminary data from Yaquina Bay, Oregon, suggests that the presence of *Z. japonica* may alter water column-benthic nutrient fluxes (Larned 2003). However, due to the strong influence of oceanic upwelling on nutrient availability and the small area of *Z. japonica* in Yaquina Bay, it is unlikely that *Z. japonica* could significantly

impact nutrient fluxes (Kaldy 2006a). The effects might be more pronounced in other estuaries with larger areal coverage of *Z. japonica*, less upwelling, and longer water residence times.

#### Fisheries Habitat Utilization

The importance of the native eelgrass, *Z. marina*, as habitat for juvenile salmonids and other commercially and recreationally important fisheries species is widely recognized (Phillips 1984; Murphy et al. 2000; Johnson et al. 2003; Fisheries and Oceans Canada 2009). To date, there has been only one published study examining fish utilization of *Z. japonica* habitat (Semmens 2008). The results of that field experiment suggests that juvenile Chinook salmon (*Oncorhynchus tshawytscha*) have a preference for the native *Z. marina* over *Z. japonica* (Semmens 2008). Due to the abundance of potential prey organisms in *Z. japonica* habitats, *Z. japonica* is likely to provide forage habitat for fisheries organisms (Posey 1988; Thom et al. 1995; Ferraro and Cole 2012). Pacific herring (*Clupea pallasii*) have been documented to use both *Z. marina* and *Z. japonica* as spawning substrate in Washington (D. Penttila, WDFW retired, unpublished data) and Oregon (Matteson 2004). In Europe, a variety of species utilize *Z. noltii* Hornem high intertidal seagrass habitat when it is flooded, including spawning herring (*Clupea harengus*) (Polte and Asmus 2006a, b). *Z. noltii* is directly analogous to *Z. japonica* with respect to plant architecture and vertical distribution (Bigley and Barreca 1982), suggesting the potential for similar fisheries species utilization of *Z. japonica* habitats in North America.

#### Migratory Waterfowl Foraging Habitat

Nineteen bird species in the Pacific Northwest are listed by Phillips (1984) as *Z. marina* consumers. The use of *Z. japonica* as foraging habitat for migratory waterfowl species is also well known (Baldwin and Lovvorn 1994a, b; Lamberson et al. 2011). A study of the feeding habits of waterfowl in Boundary Bay, British Columbia, found that *Z. japonica* comprised the largest fraction of the diet for all species (brant, American widgeon, northern pintail, and mallard) except green-winged teal (Baldwin and Lovvorn 1994a). Although *Z. marina* also comprised a large proportion of the brant diet (41 %), it was a relatively minor component (<5 %) in the diets of the other species. The preferential consumption of *Z. japonica* was attributed to its greater accessibility over the course of the tidal cycle, the higher energy content of its leaves, and easier manipulation of its smaller leaves and rhizomes (Baldwin and

Lovvorn 1994a). Brant are also undergoing a distribution shift that has been linked to changes in habitat availability along the Pacific Coast (Wilson and Atkinson 1995; Ward et al. 2005). If populations of *Z. marina* decline in brant wintering areas along the Pacific Coast (Ward et al. 2005), the importance of *Z. japonica* as an alternative food resource may increase.

#### Wading Shorebirds

There are few studies of wading shorebird utilization of seagrass habitat in the Pacific Northwest. Lamberson et al. (2011) observed shorebird utilization of *Z. japonica* and *Z. marina* in Yaquina Bay, with active foraging in *Z. japonica* beds. They found no statistically significant difference ( $P = 0.261$ ) in the density of wading shorebirds between *Z. marina* and *Z. japonica* habitat and suggested that there is no evidence that birds will be negatively impacted by the presence of *Z. japonica* (Lamberson et al. 2011).

#### Aquaculture Interactions

In Washington State, the shellfish industry has been the dominant force behind the efforts to list *Z. japonica* as a noxious weed. Based on public comments (see <http://www.ecy.wa.gov/programs/wq/pesticides/comments.html>) there is a perception that the presence of *Z. japonica* interferes with culture of the non-native Manila clam (*Ruditapes philippinarum*) on graveled tide flats. White paper reports suggest shellfish growers in Washington are experiencing economic losses due to decreased production on shellfish beds inhabited by *Z. japonica* (Fisher et al. 2011). However, due to insufficient information on the methods, numbers of replicate samples, and statistical testing, the validity of the scientific conclusions about the degree of impact of *Z. japonica* on Manila clams could not be evaluated. Fisher et al. (2011) did not examine alternative hypotheses for decreased Manila clam production (e.g., ocean acidification, indirect grazing pressure); therefore a clear cause and effect relationship between the presence of *Z. japonica* and hypothesized declines in Manila clam production has not been demonstrated.

Only a single study has evaluated the impact of *Z. japonica* presence on Manila clam production. Tsai et al. (2010) concluded that Manila clam condition (measured as meat dry weight) was reduced in the presence of *Z. japonica*. The difference in clam meat weight between *Z. japonica* presence and absence was about 100 mg (Tsai et al. 2010; J. Ruesink pers. comm.). Assuming a 40 mm adult Manila clam weighs about 600 mg (Tsai et al. 2010), this is about a 17 % decrease in meat weight. Clam shell growth was not affected by *Z. japonica* presence and plots with *Z. japonica* had increased clam recruitment relative to

removal plots (Tsai et al. 2010). Consequently, the presence of *Z. japonica* appears to affect Manila clam production; however, the economic implications have not been evaluated. Recent work in Korea concluded that mechanical Manila clam harvest stimulated *Z. japonica* sexual reproduction and that the seagrass beds recovered within about 1 year of disturbance (Park et al. 2011). That study suggests that *Z. japonica* is resilient to and may even benefit from low frequency (annual) destructive Manila clam aquaculture harvest. Consequently, it appears possible that *Z. japonica* and Manila clam aquaculture can coexist.

### Review of Relevant Laws and Policy

#### US Federal Laws and Policy

Congress has enacted several pieces of legislation to deal with aquatic invasive species (AIS); these include the Lacey Act, the Nonindigenous Aquatic Nuisance Prevention and Control Act (NANPCA) and the National Invasive Species Act (NISA). However, these laws have been criticized as inadequate to regulate AIS because they address only a limited number of introduction vectors (Nadol 1999). Consequently, States are considered the primary alternative to national AIS management (Nadol 1999); which has led to the development of an overlapping mosaic of federal and state regulations (Williams and Grosholz 2008). This mosaic is evident in the management of *Z. japonica* in North America. For example, *Z. japonica* is not listed on the Federal Invasive Species List or the Federal Noxious Weed List (Table 1). However, *Z. japonica* is listed as a noxious weed by California and Washington, and is considered invasive by California (Table 1). In contrast, Oregon does not list *Z. japonica* as an invasive species or a noxious weed. Consequently, states are left to decide the “best management practices,” which may in some cases contradict other existing state and federal policies.

A variety of federal agencies regulate activities that affect native and non-native aquatic species. Under federal regulatory policy, activities that involve construction, excavation, fill, and certain other modifications of the “waters of the US” are regulated by US Army Corps of Engineers (USACE) under Section 10 of the Rivers and Harbors Act of 1899, Section 404 of the Clean Water Act, and other regulatory policies. Seagrasses and other submerged aquatic vegetation are also protected under the Clean Water Act, 1972 (as amended), section 404(b)(1), “Guidelines for Specification of Disposal Sites for Dredged or Fill Material,” subpart E, “Potential Impacts on Special Aquatic Sites” which includes sanctuaries and refuges,

wetlands, mudflats, vegetated shallows, coral reefs, riffle, and pool complexes. In cases where projects have the potential to negatively impact wetlands and special aquatic sites, the goal of these regulatory authorities is to achieve no net loss of functions and values. The US Environmental Protection Agency (EPA) also has regulatory authority under the Clean Water Act specifically to restore and maintain oceans, watersheds, and their aquatic ecosystems to protect human health, support economic and recreational activities, and provide healthy habitat for fish, plants, and wildlife. The National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA) also plays a role in consultations under authority of the Endangered Species Act (ESA) and the Magnuson-Stevens Act (MSA). The ESA and MSA are invoked when management actions affect endangered species and essential fish habitat (EFH), respectively; for example, removal of seagrass habitat could affect endangered salmonid species. Currently, the native seagrass species *Z. marina* is considered EFH. Although NMFS-Northwest Region (NR) recognizes that *Z. japonica* can provide some of the same ecological functions as *Z. marina* and other seagrasses, NMFS-NR does not take measures to protect it, based on their interpretation of Executive Order 13112 (J. Stadler, NOAA-NMFS pers. comm., 11/07/12). This interpretation may be inconsistent with the Federal invasive species and noxious weed lists, because *Z. japonica* is not listed on either (Table 1).

### State Laws and Policy

The current California State policy is that *Z. japonica* is considered a “noxious weed” and an “invasive species” that should be controlled (Table 1). In 2003, the California Department of Fish and Game and California Sea Grant launched an effort to eradicate a small population reported in Humboldt Bay (Frimodig and Ramey 2009; Ramey et al. 2011). In 2011, the USACE issued a 5-year permit to California to allow eradication efforts to continue. One of the permit conditions specified that the effects of *Z. japonica* removal treatments would be documented; however, at the time of publication, these reports were unavailable.

Oregon currently does not identify *Z. japonica* as a noxious weed or as an invasive species (Table 1) and does not appear to take any formal stance on the status of this non-native plant in Oregon State waters. In Washington, there are a number of laws and a variety of agencies with the responsibility and authority to protect seagrass habitat. The General Master Program Provisions identifies “eelgrass beds” and “intertidal habitats with vascular plants” as critical saltwater habitats that require protection due to its ecological significance in the nearshore environment

(Washington Administrative Code (WAC) 173-26-221). These provisions specify ‘no net loss’ of ecological functions to eelgrass habitat when projects occur near shorelines and submerged areas. Washington Administrative Code (WAC 220-110-250, current language adopted in 1994 through the Washington State Register order 94-23-058 filed by WDFW) does not make a distinction between the two eelgrass species in the genus *Zostera*. In addition, *Z. marina* is listed under Priority Habitats and Species which requires protective measures for its survival due to its population status, sensitivity to habitat alteration, and/or recreational, commercial, or tribal importance (WAC 173-26-020; WDFW 2008). Eelgrass is also protected under the Washington State Environmental Policy Act that requires state and local governments to enhance ecological systems and natural resources important to the state (RCW 43.21C.010); further protection of eelgrass can be deduced in the Growth Management Act that protects critical areas defined as wetlands or fish and wildlife conservation areas (RCW 36.70A.060).

Washington State has recently undergone a reversal in seagrass protection policy. Historically, Washington State agencies protected both *Z. marina* and *Z. japonica* as seagrass habitat (WAC 220-110-250, Washington State Register order 94-23-058 filed by WDFW) and WAC 173-26-221. The apparent intention of these policies was to protect both *Zostera* congeners.

As reflected in the policy of no net loss of *Zostera* spp., resource agencies in Washington State view *Z. japonica* as providing similarly important ecological functions as are provided by *Z. marina*. Neither WDNR nor WDFW see an immediate negative effect from the spread of *Z. japonica*... Therefore, it is improbable that *Z. japonica* will be classified as a noxious weed or placed on the monitor list even though it is an invasive exotic species. (Pawlak 1994)

As of March 2011, WDFW announced it would only protect *Z. marina* habitat under the WDFW Priority Habitats and Species List while explicitly excluding *Z. japonica* (<http://www.caseinlet.org/uploads/Blake2.8.11Zosterajaponica.pdf>); a move that may be inconsistent with the current wording of WAC 220-110-250 from 1994. In June 2013, the WDFW proposed to change the language of WAC 220-110-250 to specifically exclude *Z. japonica* (Washington Department of Ecology 2013). This management reversal appears to have been a political concession to shellfish growers who have rallied support against the legal protection of *Z. japonica* (Banse 2011). The shellfish industry is largely exempt from regulation by WDFW regardless of impact to either native or non-native seagrass (R. Carman, WDFW, pers. comm.). However, the industry is subject to “no net loss” provisions of Shoreline Management Plans and

regulation by the USACE (M. Goehring, WDNR, pers. comm.). Consequently, failure of state agencies to protect *Z. japonica* habitat may be inconsistent with existing Washington State Administrative codes.

In early 2012, the Washington State Noxious Weed Control Board (NWCB) identified *Z. japonica* as a class C noxious weed on commercially managed shellfish beds only (WAC 16-75-015, Table 1). Late in 2012, the Washington NWCB accepted a proposal to list *Z. japonica* as a noxious weed throughout the State. In late 2013, the NWCB will be considering two new proposals; one to remove *Z. japonica* from the noxious weed list and another to revert back to the listing only for commercial shellfish beds (A. Halpern, NWCB, pers. comm.). Consequently, there will be no clear path for management of *Z. japonica* within Washington State waters until the resource agencies and constituents come to a clear consensus.

#### Applicable Canadian Laws and Policy

Canadian agencies, ministries, and provincial governments share responsibility for invasive species management in Canada. The Canadian government has developed an action plan (<http://www.dfo-mpo.gc.ca/science/enviro/ais-eae/plan/plan-eng.htm>) to address the threat of AIS and a mechanism for assessing potential impacts of introductions (<http://www.dfo-mpo.gc.ca/science/enviro/ais-eae/code/prelim-eng.htm>). A 2008 internal evaluation criticized the program for a lack of governance framework and undefined accountabilities, roles and responsibilities (<http://www.dfo-mpo.gc.ca/ae-ve/evaluations/08-09/6b080-eng.htm>).

In Canada, protection for seagrass is predicated upon fisheries utilization; section 35 of the Canadian Federal Fisheries Act states that “no person shall carry on any work or undertaking that results in the harmful alteration, disruption or destruction of fish habitat.” (Ministry of Justice 2011). “Fish habitat” is defined as “spawning grounds and nursery, rearing, food supply and migration areas on which fish depend directly or indirectly in order to carry out their life processes” (Section 34(1); Ministry of Justice 2011). A synthesis of available research by Fisheries and Oceans Canada (DFO) has identified *Z. marina* as an Ecologically Significant Species (ESS) (Fisheries and Oceans Canada 2009). The criteria that established eelgrass as an ESS was based on the habitat structure it provides, the support of other organisms, and its wide distribution and abundance throughout Canadian waters (Fisheries and Oceans Canada 2009). We were unable to find any record of an ESS designation for *Z. japonica*.

#### Methods for *Z. japonica* Control

Discussions on how to respond to the spread of *Z. japonica* in North America have been ongoing for several decades. Currently, management activities in the United States relating to *Z. japonica* are disparate and predominantly geared toward control and eradication. *Z. japonica* removal/control policies contradict efforts to conserve and protect seagrass in other regions of the US and around the world (Orth et al. 2006a).

A variety of methods to eradicate *Z. japonica* have been attempted; such as spraying herbicide, covering the grass with plastic sheets or burlap, and physical removal of roots (Frimodig and Ramey 2009). Heat treatments such as propane flamethrowers, infrared radiant heat, cartridge heaters, and hot water weed control systems have also been tested in California (Ramey et al. 2011). Although these methods have decreased the area of *Z. japonica*, after almost a decade of intensive effort, the goal of complete eradication in Humboldt Bay, California, has not been achieved while the areal distribution of patches has continued to expand (Ramey et al. 2011).

Currently, the Washington State Department of Ecology is developing a National Pollution Discharge Elimination System (NPDES) permit for the use of the herbicide imazamox to control *Z. japonica* on commercial shellfish beds in estuarine waters (<http://www.ecy.wa.gov/programs/wq/pesticides/eelgrass.html>). Imazamox is the active ingredient in the herbicide Clearcast<sup>®</sup>, labeled for use in the aquatic environment (US EPA 2008, 2012), despite the lack of evidence for efficacy on estuarine plants and major data gaps with regard to effects on estuarine/marine fish, shrimp, and mollusks (US EPA 1997). Imazamox inhibits production of the plant enzyme acetolactate synthetase, which prevents the formation of the essential amino acids valine, leucine, and isoleucine (Mallory-Smith and Retzinger 2003). This mechanism of action is not specific to *Z. japonica* and may have a negative effect on other photosynthetic organisms (e.g., native eelgrass, macroalgae, phytoplankton, and microphytobenthos). We were unable to identify any peer-reviewed studies describing the effect of imazamox or Clearcast<sup>®</sup> on marine or estuarine phytoplankton, benthic microalgae, macroalgae, or seagrass.

Federal and state resource agencies and citizen groups have expressed concerns about the potential for herbicide application to cause un-intended impacts to non-target organisms such as *Z. marina* and listed endangered species (ESA) such as salmonids (<http://www.ecy.wa.gov/programs/wq/pesticides/comments.html>). Preliminary field-based testing indicates that downstream *Z. marina* is negatively impacted by the herbicide applications to *Z. japonica* beds (J. Gaeckle, pers.

obs.). Chemical control measures applied to *Z. japonica* would therefore most likely result in loss of the native seagrass *Z. marina*. Due to the protection measures afforded *Z. marina* under the MSA and other federal and state regulations, mitigation could be required for any loss of *Z. marina* that occurred as a result of *Z. japonica* control activities.

## Conclusions and Recommendations

The ecological and economic effects of some introduced species, like *Z. japonica*, are not easily characterized. The current range of management approaches in North America indicates there is little consensus among stakeholders, resource managers or between state and international governments with regard to appropriate management of *Z. japonica*. It is considered harmful by some, while others consider it benign or beneficial. The contrasting views reflect the diversity of value systems in our society, and contribute to the complexity of resource management decisions. In general, there is a need for stronger federal leadership on introduced aquatic species along with a concerted effort to develop clear, consistent and scientifically sound policies between federal and state regulatory and management agencies.

Conflicting management strategies may be due in part to a lack of adequate scientific information provided to resource managers responsible for invasive species management decisions (Stocker 2004; Williams and Grosholz 2008). Inventories that describe the amount and location of resources (e.g., seagrass distribution maps) are critical to the development of management policy (Mumford 1994). However, baseline data on the distribution and areal extent of *Z. japonica* beds on the Pacific Coast are limited to a few areas in Washington (Bulthuis 1995; Gaeckle et al. 2011), Oregon (Young et al. 2008), and British Columbia (Gillespie 2007). The Washington State Department of Natural Resources has conducted surveys of seagrass distribution and abundance in Greater Puget Sound since 2000 (Gaeckle et al. 2011); however, due to methodological constraints, changes in the distribution and area of *Z. japonica* populations cannot be evaluated from this database. Consequently, there is a need to better understand the physiology, ecology, and distribution of this seagrass in order to predict its colonization potential and develop proactive monitoring and prevention programs if necessary.

State level management policies which do not differentiate between the native and introduced *Zostera* seagrasses on the Pacific coast were presumably based on assumptions regarding the positive habitat value of seagrasses (Pawlak 1994). Although the importance of the native eelgrass *Z. marina* to commercially and

recreationally important fisheries species is well-known (Johnson et al. 2003), the potential habitat value of *Z. japonica* for commercially and recreationally valuable fisheries species remains largely unexplored (Pawlak 1994; Semmens 2008; Mach et al. 2010). Consequently, there remains a critical need for data on the fisheries habitat utilization and other ecological services provided by *Z. japonica* that could be used to provide a basis for better informed management policies.

Ecosystem level management decisions are being driven largely by concerns over impacts to aquaculture operations, although there is little scientific data to support the need for the proposed actions. Alternative hypotheses (e.g., ocean acidification and indirect grazing) have not been adequately evaluated. The expansion of *Z. japonica* beds on commercial shellfish grounds in Washington may have been facilitated by applications of the pesticide carbaryl used to control burrowing shrimp (Dumbauld and Wyllie-Echeverria 2003). The abundance of *Z. japonica* within these commercial shellfish grounds could therefore decline if carbaryl pesticide applications were phased out as planned at the end of 2012 (Schreder 2003). Further, the evidence to support economic losses to shellfish growers in Washington due to the presence of *Z. japonica* is not well quantified, and evidence from its native range suggests that Manila clam aquaculture and *Z. japonica* populations can coexist (Park et al. 2011).

Invasive species eradication is generally only effective when populations are small and restricted, there are adequate financial resources and action is taken early in the colonization phase (Williams and Grosholz 2008). *Z. japonica* does not meet these criteria in most Pacific Northwest estuaries. Due to the sheer size and extent of the *Z. japonica* populations in most areas of Washington and Oregon, eradication of established populations would not be possible, even if it were deemed desirable. However, control of *Z. japonica* by a variety of methods, both chemical and non-chemical, may be possible within limited areas, and this may address the concerns posed by shellfish growers. Managers should recognize that regardless of the control method chosen, it is likely to be a labor-intensive and costly endeavor requiring constant maintenance, because *Z. japonica* populations are capable of rapid recovery following the cessation of disturbance (Park et al. 2011). The extent of other ecological impacts that occur as a result of controlling *Z. japonica* is unknown. The decision to implement *Z. japonica* control methods, either chemical or non-chemical, should be based on a thorough understanding of the economic and ecosystem costs associated with the presence of this species, balanced by an understanding of the extent of environmental degradation caused by control efforts. Much of this information is currently lacking (Pawlak 1994; Mach et al. 2010).

## Recommended Actions

Given the large number of invasive species already established in this country, the increasing frequency of new invasions, and the limited financial resources available, managers must set priorities to determine which species warrant immediate response, which deserve secondary consideration if time and funding permit, and which may be ignored (Byers et al. 2002). We recommend the following actions to fill some of the existing data gaps and help provide resource managers with the information they need to balance complex trade-offs between economic development and the risks of ecosystem degradation.

1. Conduct a risk/benefit analysis as suggested by Beck et al. (2008) to determine whether further regulatory action is warranted with regard to *Z. japonica*.
2. Conduct independent, peer-reviewed research using rigorous experimental design and statistical analysis procedures to evaluate:
  - a. efficacy of proposed herbicide applications
  - b. potential impacts of herbicides to target and non-target marine/estuarine primary producers (e.g., *Z. marina*, planktonic and benthic microalgae and macroalgae)
  - c. potential for herbicide to persist in estuarine food chains.
3. Conduct a cost–benefit analysis to determine where specific management actions (e.g., eradication efforts) are most likely to be effective. Incorporating economic considerations into the management of non-native species may influence optimal management strategies (Buhle et al. 2005; Williams and Grosholz 2008).
4. Investigate the environmental impacts of both chemical and non-chemical *Z. japonica* control efforts on native benthic communities, waterfowl foraging opportunities, fisheries habitat utilization and other components of affected ecosystems. To date this has received little consideration.
5. Document the ecosystem services (e.g., fisheries habitat utilization, shoreline stabilization, carbon sequestration, etc.) provided by *Z. japonica*. In particular, there is a need to investigate the potential use of *Z. japonica* by spawning herring, juvenile salmonids, and other commercial and recreationally important fisheries species.
6. Identify the major dispersal pathways for *Z. japonica* and the relative importance of vegetative versus sexual reproduction in the establishment of new colonies.
7. Model the colonization potential of *Z. japonica* based on physiological tolerances (e.g., temperature, salinity, nutrients, etc.) and dispersal mechanisms.

8. Develop and evaluate alternative aquaculture practices that can coexist with seagrass.

**Acknowledgments** The authors thank the following individuals for valuable comments and discussion on draft versions of this manuscript, H. Berry, R. Carman P. Dowty, B. Dumbauld, M. Goehring, L. Nelson, W. Nelson, F. Short, B. Reeves, R. Virnstein, S. Yost, and four anonymous reviewers. Authors also thank J. Ruesink for access to Manila clam weight data. The information in this document has been funded in part by the U.S. Army Corps of Engineers and Environmental Protection Agency. It has been subjected to review by the National Health and Environmental Effects Research Laboratory's Western Ecology Division and by the US Army Corps of Engineers, Environmental Research and Development Center and approved for publication. Approval does not signify that the contents reflect the views of the agencies, nor does mention of trade names or commercial products constitute endorsement or recommendation for use.

## References

- Abe M, Yokota K, Kurashima A, Maegawa M (2010) Estimation of light requirement for growth of *Zostera japonica* cultured seedlings based on photosynthetic properties. *Fish Sci* 76:235–242
- Baldwin JR, Lovvorn JR (1994a) Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Mar Ecol Prog Ser* 103:119–127
- Baldwin JR, Lovvorn JR (1994b) Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. *Mar Biol* 120:627–638
- Bando KJ (2006) The roles of competition and disturbance in a marine invasion. *Biol Invasions* 8:755–763
- Banse T (2011) <http://kplu.org/post/invasive-eelgrass-doesnt-follow-usual-invaders-script>, <http://kplu.org/post/board-classifies-perple-xing-invader-japanese-eelgrass-noxious-weed>. Accessed 13 July 2012
- Beck KG, Zimmerman K, Schardt JD, Stone J, Lukens RR, Reichard S, Randall J, Cangelosi AA, Cooper D, Thompson JP (2008) Invasive species defined in policy context: recommendations from the Federal Invasive Species Advisory Committee. *Invasive Plant Sci Manag* 1:414–421
- Bigley RE, Barreca JL (1982) Evidence for synonymizing *Zostera americana* den Hartog with *Zostera japonica* Aschers & Graebn. *Aquat Bot* 14:349–356
- Britton-Simmons KH, Wyllie-Echeverria S, Day EK, Booth KP, Cartwright K, Flores SGC, Higgins TL, Montanez C, Ram A, Welch KM, Wyllie-Echeverria V (2010) Distribution and performance of the nonnative seagrass *Zostera japonica* across a tidal height gradient on Shaw Island, Washington. *Pac Sci* 64:187–198
- Buhle ER, Margolis M, Ruesink JL (2005) Bang for buck: cost-effective control of invasive species with different life histories. *Ecol Econ* 52:355–366
- Bulthuis DA (1995) Distribution of seagrasses in a North Puget Sound estuary: Padilla Bay, Washington, USA. *Aquat Bot* 50:99–105
- Byers JE, Reichard S, Randall JM, Parker IM, Smith CS, Lonsdale WM, Atkinson IAE, Seastedt TR, Williamson M, Chornesky E, Hayes D (2002) Directing research to reduce the impacts of nonindigenous species. *Conserv Biol* 16:630–640
- Charalambidou I, Santamaria L, Langevoord O (2003) Effect of ingestion by five avian dispersers on the retention time, retrieval

- and germination of *Ruppia maritima* seeds. *Funct Ecol* 17:747–753
- Colautti RI, MacIsaac HJ (2004) A neutral terminology to define 'invasive' species. *Divers Distrib* 10:135–141
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annu Rev Ecol Evol Syst* 34:183–211
- Dean E, Hrusa F, Leppig G, Sanders A, Ertter B (2008) Catalogue of nonnative vascular plants occurring spontaneously in California beyond those addressed in the Jepson Manual—Part II. *Madroño* 55:93–112
- Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M (1989) Biological invasions: a global perspective. Wiley, New York, p 525
- Dudoit CM (2006) The distribution and abundance of a non-native eelgrass, *Zostera japonica*, in Oregon estuaries. Senior Thesis, Zoology Dept, Oregon State University, Corvallis, Oregon
- Dumbauld BR, Wyllie-Echeverria S (2003) The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquat Bot* 77:27–42
- Ewanchuk PJ, Williams SL (1996) Survival and re-establishment of vegetative fragments of eelgrass (*Zostera marina*). *Can J Bot* 74:1584–1590
- Ferraro SP, Cole FA (2012) Ecological periodic tables for benthic macrofaunal usage of estuarine habitats: insights from a case study in Tillamook Bay, Oregon, USA. *Estuar Coast Shelf Sci* 102–103:70–83
- Figuerola J, Green AJ (2002) Dispersal of aquatic organisms by waterbirds: a review of past research and priorities for future studies. *Freshw Biol* 47:482–494
- Figuerola J, Green AJ, Santamaria L (2002) Comparative dispersal effectiveness of widgeongrass seeds by waterfowl wintering in south-west Spain: quantitative and qualitative aspects. *J Ecol* 90:989–1001
- Fisher JP, Bradley T, Patton K (2011) Invasion of Japanese eelgrass, *Zostera japonica* in the Pacific Northwest: a preliminary analysis of recognized impacts, ecological functions, and risks. Unpublished report prepared for the Willapa-Grays Harbor Oyster Growers Association, Ocean Park, WA. [http://nwcba.gov/siteFiles/Japonica\\_White\\_Paper.pdf](http://nwcba.gov/siteFiles/Japonica_White_Paper.pdf)
- Fisheries and Oceans Canada (DFO) (2009) Does eelgrass (*Zostera marina*) meet the criteria as an ecologically significant species? Fisheries and Oceans Canada. Canadian Science Advisory Secretariat, Science Advisory Report 2009/018, P 11
- Fourqurean JW, Duarte CM, Kennedy H, Marbà N, Holmer M, Matea MA, Apostolaki ET, Kendrick G, Krause-Jensen D, McGlathery KJ, Serrano O (2012) Seagrass ecosystems as a globally significant carbon stock. *Nat Geosci* 1477:1–5. doi:10.1038/NGEO1477
- Frimodig A, Ramey K (2009) Eel grass: beneath the surface. *Outdoor California*: January–February 6–11
- Gaekle J, Dowty P, Berry H, Ferrier L (2011) Puget sound submerged vegetation monitoring project 2009 report. Washington State Department of Natural Resources Nearshore Habitat Program, Olympia. [http://www.dnr.wa.gov/ResearchScience/Topics/AquaticHabitats/Pages/aqr\\_nrsh\\_eelgrass\\_monitoring.aspx](http://www.dnr.wa.gov/ResearchScience/Topics/AquaticHabitats/Pages/aqr_nrsh_eelgrass_monitoring.aspx)
- Ganter B (2000) Seagrass (*Zostera* spp.) as food for brant geese (*Branta bernicla*): an overview. *Helgol Mar Res* 54:63–70
- Gillespie GE (2007) Distribution of non-indigenous intertidal species on the Pacific Coast of Canada. *Nippon Suisan Gakkaishi* 73:1133–1137
- Green EP, Short FT (2003) World atlas of seagrasses. University of California Press, Berkeley, California, p 298
- Hahn DR (2003a) Changes in community composition and ecosystem processes associated with biological invasions: impacts of *Zostera japonica* in the marine intertidal zone. PhD dissertation, University of Washington, Dept of Biology, Seattle, WA
- Hahn DR (2003b) Alteration of microbial community composition and changes in decomposition associated with an invasive intertidal macrophyte. *Biol Invasions* 5:45–51
- Hall LM, Hanisak MD, Virmstein RW (2006) Fragments of the seagrasses *Halodule wrightii* and *Halophila johnsonii* as potential recruits in Indian River Lagoon, Florida. *Mar Ecol Prog Ser* 310:109–117
- Harrison PG (1976) *Zostera japonica* Aschers. & Graebn. in British Columbia, Canada. *Syesis* 9:359–360
- Harrison PG (1982a) Spatial and temporal patterns in abundance of two intertidal seagrasses, *Zostera americana* den Hartog and *Zostera marina* L. *Aquat Bot* 12:305–320
- Harrison PG (1982b) Seasonal and year-to-year variation in mixed intertidal populations of *Zostera japonica* Aschers. & Graebn. and *Ruppia maritima* L. S.L. *Aquat Bot* 14:357–371
- Harrison PG (1987) Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response to intertidal invertebrates. *Estuar Coast Shelf Sci* 24:799–812
- Harrison PG, Bigley RE (1982) The recent introduction of the seagrass *Zostera japonica* Aschers & Graebn to the Pacific coast of North America. *Can J Fish Aquat Sci* 39:1642–1648
- Harwell MC, Orth RJ (2002) Long-distance dispersal potential in a marine macrophyte. *Ecology* 83:3319–3330
- Hayashida F (2000) Vertical distribution and seasonal variation of eelgrass beds in Iwachi Bay, Izu Peninsula, Japan. *Hydrobiologia* 428:179–185
- Hitchcock CL, Cronquist A, Ownbey M, Thompson JW (1969) Vascular plants of the Pacific Northwest. Part 1. University of Washington Press, Seattle, p 914
- Invasive Species Advisory Committee (2006) Invasive species definition clarification and guidance white paper. <http://www.invasivespeciesinfo.gov/docs/council/isacdef.pdf>. Accessed 25 Apr 2012
- Johnson SW, Murphy ML, Csepp DJ, Harris PM, Thedinga JF (2003) A survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska. NOAA Technical Memorandum NMFS-AFSC-139:1–48
- Kaldy JE (2006a) Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Aschers & Graebn) in a Pacific Northwest estuary, USA. *Hydrobiologia* 553:210–217
- Kaldy JE (2006b) Carbon, nitrogen, phosphorus and heavy metal budgets: how large is the eelgrass (*Zostera marina* L.) sink in a temperate estuary? *Mar Pollut Bull* 52:342–353
- Kaldy JE, Shafer DJ (2012) Effects of salinity on survival of the exotic seagrass *Zostera japonica* subjected to extreme high temperature stress. *Bot Mar* 56:75–82
- Lamberson JO, Frazier MR, Nelson WG, Clinton PJ (2011) Utilization patterns of intertidal habitats by birds in Yaquina Estuary, Oregon. US Environmental Protection Agency, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division, Newport, OR. EPA/600/R-11/118
- Larned ST (2003) Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary. *Mar Ecol Prog Ser* 254:69–80
- Lee II H, Brown CA (eds) (2009) Classification of regional patterns of environmental drivers and benthic habitats in Pacific Northwest estuaries US EPA, Office of Research and Development, National Health and Environmental Effects Research Laboratory, Western Ecology Division EPA/600/R-09/140
- Lee SY, Oh JH, Choi CI, Suh Y, Mukai H (2005) Leaf growth and population dynamics of intertidal *Zostera japonica* on the western coast of Korea. *Aquat Bot* 83:263–280



- Lindsay CE, Simons D (1997) The fisheries for Olympia Oysters, *Ostreola conchaphila*; Pacific Oysters, *Crassostrea gigas*; and Pacific Razor Clams, *Siliqua patula*, in the State of Washington, pp 89–114. In: MacKenzie CL Jr, Burrell VG Jr, Rosenfield A, Hobart WL (eds) The history, present condition, and future of the molluscan fisheries of north and central America and Europe. Volume 2, Pacific Coast and supplemental topics. NOAA technical Report NMFS 128, Department of Commerce, Washington DC, p 217
- Mach ME, Wyllie-Echeverria S, Ward JR (2010) Distribution and potential effects of a non-native seagrass in Washington State *Zostera japonica* Workshop, Friday Harbor Laboratories, San Juan Island, WA, p 37. [http://www.dnr.wa.gov/Publications/aqr\\_zostera\\_study.pdf](http://www.dnr.wa.gov/Publications/aqr_zostera_study.pdf)
- Mallory-Smith CA, Retzinger EJ Jr (2003) Revised classification of herbicides by site of action for weed resistance management strategies. *Weed Technol* 17:605–619
- Mateo MA, Cebrian J, Dunton K, Mutchler T (2006) Carbon flux in seagrasses. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, The Netherlands, pp 159–192
- Matteson K (2004) Commercial Pacific herring fishery Yaquina Bay Oregon, 2004 Summary Report. Marine Resources Program, Oregon Department of Fish and Wildlife, Newport, Oregon, p 18
- Ministry of Justice (2011) Fisheries Act. Revised statutes of Canada 1985, c. F-14. <http://laws-lois.justice.gc.ca>, and <http://laws-lois.justice.gc.ca/eng/acts/F-14/page-8.html#docCont>
- Mumford TF (1994) Inventory of seagrasses: critical needs for biologists and managers. In: Wyllie-Echeverria S, Olsen AM, and Hershman MJ (eds) Seagrass science and policy in the Pacific Northwest: proceedings of a seminar series. EPA 910/R-94-004, pp 29–37
- Murphy ML, Johnson SW, Csepp DJ (2000) A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. *Alask Fish Res Bull* 7:11–21
- Nadol V (1999) Aquatic invasive species in the coastal West: an analysis of State regulation within a Federal framework. *Environ Law* 29:339–375
- Nakaoka M, Aioi K (2001) Ecology of seagrasses *Zostera* spp. (Zosteraceae) in Japanese waters: a review. *Otsuchi Mar Sci* 26:7–22
- Nomme KM, Harrison PG (1991) Evidence of interaction between the seagrasses *Zostera marina* and *Zostera japonica* on the Pacific coast of Canada. *Can J Bot* 69:2004–2010
- Occhipinti-Ambrogi A, Galil BS (2004) A uniform terminology on bioinvasions: a chimera or an operative tool? *Mar Pollut Bull* 49:688–694
- Orth RJ, Luckenbach ML, Moore KA (1994) Seed dispersal in a marine macrophyte: implications for colonization and restoration. *Ecology* 75:1927–1939
- Orth RJ, Carruthers TJB, Dennison WC, Duarte CM, Fourqurean JW, Heck KL, Hughes AR, Kendrick GA, Kenworthy WJ, Olyarnik S, Short FT, Waycott M, Williams SL (2006a) A global crisis for seagrass ecosystems. *Bioscience* 56:987–996
- Orth RJ, Harwell MC, Inglis GJ (2006b) Ecology of seagrass seeds and seagrass dispersal processes. In: Larkum AWD, Orth RJ, Duarte CM (eds) Seagrasses: biology, ecology and conservation. Springer, The Netherlands, pp 111–133
- Park SR, Kim YK, Kim JH, Kang CK, Lee KS (2011) Rapid recovery of the intertidal seagrass *Zostera japonica* following intense Manila clam (*Ruditapes philippinarum*) harvesting activity in Korea. *J Exp Mar Biol Ecol* 407:275–283
- Pawlak BT (1994) Analysis of the policies and management practices of Washington State agencies as they pertain to seagrasses, *Zostera marina* and *Zostera japonica*. Report to Padilla Bay National Estuarine Research Reserve, Padilla Bay National Estuarine Research Reserve Reprint Series, No 20, p 20
- Phillips RC (1984) The ecology of eelgrass meadows in the Pacific Northwest: a community profile. FWS/OBS-84/24 US Dept. of the Interior, Washington, DC
- Polte P, Asmus H (2006a) Intertidal seagrass beds (*Zostera noltii*) as spawning grounds for transient fishes in the Wadden Sea. *Mar Ecol Prog Ser* 312:235–243
- Polte P, Asmus H (2006b) Influence of seagrass beds (*Zostera noltii*) on the species composition of juvenile fishes temporarily visiting the intertidal zone of the Wadden Sea. *J Sea Res* 55:244–252
- Posey MH (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* 69:974–983
- Quayle DB (1953) Oyster Bulletin 4(1). British Columbia Dept of Fisheries, Shellfish Laboratory, Ladysmith, BC, p 15
- Quayle DB (1964) Distribution of introduced marine mollusca in British Columbia waters. *J Fish Res Board Can* 21:1155–1181
- Ramey K, Schlosser S, Manning S (2011) *Zostera japonica* eradication Project Annual Report: 2010. Extension Publications, California Sea Grant College Program, UC San Diego. <http://escholarship.org/uc/item/1fh8t6vv>
- Rejmanek M (1995) What makes a species invasive? In: Pysek P, Prach K, Rejmanek M, Wade PM (eds) Plant invasions. SPB Academic Publishing, The Hague, Netherlands, pp 3–13
- Reusch TBH (2002) Microsatellites reveal high population connectivity in eelgrass (*Zostera marina*) at two contrasting coastal areas. *Limnol Oceanogr* 47:78–85
- Rivers DO, Short FT (2007) Effect of grazing by Canada geese *Branta canadensis* on an intertidal eelgrass *Zostera marina* meadow. *Mar Ecol Prog Ser* 333:271–279
- Ruckelshaus MH (1996) Estimation of genetic neighborhood parameters from pollen and seed dispersal in the marine angiosperm *Zostera marina* L. *Evolution* 50:856–864
- Ruesink JL, Hong JS, Wisheart L, Hacker SD, Dumbauld BR, Hessian-Lewis M, Trimble AC (2010) Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary. *Biol Invasions* 12:1773–1789
- Sayce CS (1976) The oyster industry of Willapa Bay. In: Andrews RD III, Carr RL, Gibson F, Lang BZ, Soltero RA, Swedberg KC (eds) Proceedings of the symposium on terrestrial and aquatic ecological studies of the northwest. Eastern Washington State College Press, Cheney, WA, pp 347–356
- Schreder E (2003) Carbaryl use in Willapa Bay and Grays Harbor to end—settlement phases out insecticide, seeks alternatives. Washington toxics coalition. *Alternatives* 22:1–2
- Semmens BX (2008) Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. *Can J Fish Aquat Sci* 65:2053–2062
- Shafer DJ (2007) Physiological factors affecting the distribution of the nonindigenous seagrass *Zostera japonica* along the Pacific coast of North America. Dissertation, University of South Alabama, p 134
- Shafer DJ, Wyllie-Echeverria S, Sherman TD (2008) The potential role of climate in the distribution and zonation of the introduced seagrass *Zostera japonica* in North America. *Aquat Bot* 89:297–302
- Shafer DJ, Kaldy JE, Sherman TD, Marko KM (2011) Effects of salinity on photosynthesis and respiration of the seagrass *Zostera japonica*: a comparison of two established populations in North America. *Aquat Bot* 95:214–220
- Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:S159–S169

- Short FT, Wyllie-Echeverria S (1996) Natural and human-induced disturbances of seagrasses. *Environ Conserv* 23:17–29
- Stocker RK (2004) The management of invasive plants in the United States: are scientists providing what managers need? *Weed Technol* 18:1528–1532
- Thom RM (1990) Spatial and temporal patterns in plant standing stock and primary production in a temperate seagrass system. *Bot Mar* 33:497–510
- Thom RM, Miller B, Kennedy M (1995) Temporal patterns of grazers and vegetation in a temperate seagrass system. *Aquat Bot* 50:201–205
- Thom RM, Borde AB, Blanton SL, Woodruff DL, Williams GD (2001) The influence of climate variation and change on structure and processes in nearshore vegetated communities of Puget Sound and other Northwest estuaries. In: Droscher T (ed) Proceedings of the 2001 Puget sound research conference, Puget sound water quality action team, Olympia, WA
- Thomsen SM (2010) Experimental evidence for positive effects of invasive seaweed on native invertebrates via habitat-formation in a seagrass bed. *Aquat Invasions* 5:341–346
- Tsai C, Yang S, Trimble AC, Ruesink JL (2010) Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. *Mar Biol* 157:1929–1936
- US Environmental Protection Agency (1997) Pesticide fact sheet: Imazamox. US EPA, Office of Pesticide Programs, Arlington, VA. <http://www.epa.gov/opprd001/factsheets/imazamox.pdf>
- US Environmental Protection Agency (2008) Environmental fate and ecological risk assessment-registration of new use Imazamox for the proposed new use for the control of vegetation in and around aquatic and non-cropland sites. USEPA PC Code 129171. <http://www.regulations.gov/#!documentDetail;D=EPA-HQ-OPP-2009-0081-0112>
- US Environmental Protection Agency (2012) Label amendment—revise voluntary restriction. Office of Chemical Safety and Pollution Prevention, Registration Division. [http://www.epa.gov/pesticides/chem\\_search/ppls/000241-00437-20120320.pdf](http://www.epa.gov/pesticides/chem_search/ppls/000241-00437-20120320.pdf)
- Ward DH, Reed A, Sedinger JS, Black JM, Derksen D, Castelli PM (2005) North America Brant: effects of changes in habitat and climate on population dynamics. *Glob Change Biol* 11:869–880
- Washington Department Fish and Wildlife (2008) Priority habitat and species list. Olympia, WA, p 177. <http://wdfw.wa.gov/publications/00165/wdwwf00165.pdf>
- Washington Department of Ecology (2013) The current regulatory landscape for *Zostera japonica* in Washington State. Prepared for *The Science and Management of Zostera japonica in Washington State* agency meeting, 18–19 June, p 3
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes RA, Kendrick GA, Kenworthy JW, Short FT, Williams SL (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc Natl Acad Sci* 106:12377–12381
- Willette DA, Ambrose RF (2009) The distribution and expansion of the invasive seagrass *Halophila stipulacea* in Dominica, West Indies, with a preliminary report from St Lucia. *Aquat Bot* 91:137–142
- Williams SL (2007) Introduced species in seagrass ecosystems: status and concerns. *J Exp Mar Biol Ecol* 350:89–110
- Williams SL, Grosholz ED (2008) The invasive species challenge in estuarine and coastal environments: marrying management and science. *Estuaries Coasts* 31:3–20
- Williamson M (1996) Biological invasions. Chapman and Hall, London
- Wilson UW, Atkinson JB (1995) Black Brant winter and spring-staging use at two Washington coastal areas in relation to eelgrass abundance. *Condor* 97:91–98
- Wonham MJ, O'Connor M, Harley CDG (2005) Positive effects of a dominant invader on introduced and native mudflat species. *Mar Ecol Prog Ser* 289:109–116
- Young DR, Clinton PJ, Specht DT, DeWitt TH, Lee H II (2008) Monitoring the expanding distribution of nonindigenous dwarf eelgrass *Zostera japonica* in a Pacific Northwest USA estuary using high resolution digital aerial photography. *Spatial Sci* 53:87–97