

Distribution and potential effects of a non-native
seagrass in Washington State

Zostera japonica Workshop

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Taxonomic History of *Zostera japonica* in the Pacific Northwest

The species now known as *Zostera japonica* has undergone many changes in taxonomic nomenclature in the Pacific Northwest since its first record of collection by N. Hotchkiss in 1957 (WTU - 208020). This sample was identified as *Zostera nana* Roth by Hitchcock (1969) who stated it was "...supposedly introduced in our area..." In 1970 den Hartog (1970) described the same sample collected by Hotchkiss in 1957 as new species and named it *Zostera americana* den Hartog.

The University of Washington Herbarium includes collections of two species of native seagrass (*Zostera marina*, a low intertidal and subtidal species, and *Ruppia maritima*, a high intertidal and brackish water species) from western Washington counties. Specimens were collected in the late 1800s, associated with early exploration, and again in the 1930s when C.L. Hitchcock was writing his Flora of the Pacific Northwest. The 1957 record of *Z. japonica* occurred during a collection gap for seagrasses in the 1940s-1970s, and all three species have appeared in recent collections (Figure 1).

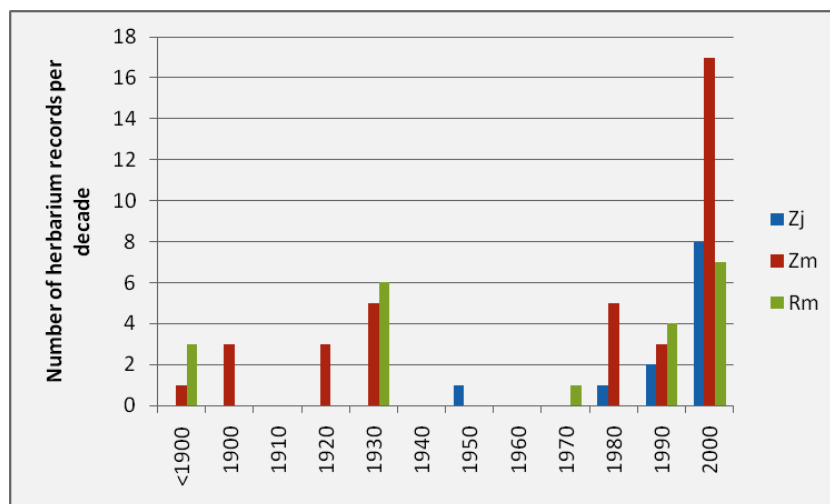


Figure 1: Records of three seagrasses in western Washington counties, compiled by decade, from the University of Washington Herbarium, <http://www.washington.edu/burkemuseum/collections/herbarium/index.php>. Zj = *Zostera japonica*, Zm = *Zostera marina*, Rm = *Ruppia maritima*.

Phillips and Shaw (1976) resampled *Z. americana* populations of a small, intertidal seagrass in Washington and compared these to collections of *Z. noltii* Hornem from England and den Hartog's illustrations of *Z. noltii*. They argued that *Z. americana*'s identifying morphological characteristics were too variable to differentiate between the two species and concluded the Washington *Z. americana* should be called *Z. noltii*. In that same year, Harrison (1976), argued that den Hartog's illustrations of *Z. japonica*'s Aschers. & Graebn. key characteristics did not differ from those described for *Z. americana* and concluded the plants were truly *Z. japonica*, likely introduced from Japan as packing material for transporting oysters. Harrison's conclusions

were later supported by Bigley & Barreca (1982), who compared morphological characteristics of four morphologically similar *Zostera* species using principal components analysis. Their results suggested that the species in Washington and British Columbia was *Z. japonica* and that den Hartog identified *Z. americana* on geographical rather than morphological traits, as both *Z. japonica* and *Z. noltii* originate at great distance from the eastern North Pacific.

In 2001, Tomlinson and Posluzny (2001) used four discrete groups of vegetative and reproductive features of plants within *Zosteraceae* to describe one new genus, *Zosterella*, with four subgenera. This replaced the previous description of two genera, *Heterozostera* and *Zostera*, with *Zostera*, having two subgenera, *Zostera* and *Zosterella*. Subsequently, *Z. japonica* was renamed *Nanozostera japonica* Ashers. & Graebn. Tanaka et al. (2003) renamed *N. japonica* to *Zostera japonica* after a molecular phylogenetic tree based on matK sequence data failed to support Tomlinson and Posluzny's (2001) assertions.

In addition to the confusion over its scientific nomenclature, *Z. japonica* has been referred to by many common names. This, too, may cause much confusion as this species expands its range in the Pacific Northwest and scientists and managers along the coast first encounter a novel species. Common names for *Z. japonica* include, but are not limited to, Asian eelgrass, duck grass, dwarf eelgrass, Japanese eelgrass, eelgrass & narrow-bladed eelgrass.

A note on non-native/invasive terminology

Inconsistent and imprecise use of terminology regarding species introductions has led to divergent interpretations of published literature and to confusion on invasion theory. There have been some recent attempts to standardize terminology in invasion ecology (e.g., Colautti and MacIsaac 2004, Occhipinti-Ambrogi and Galil 2004, Carlton 2009).

Non-indigenous Species: Any species that is intentionally or unintentionally moved by human activities beyond its natural range or natural zone of potential dispersal.

Synonyms: alien, immigrant, introduced, non-native, exotic

Established Species: A species with one or more successfully reproducing (i.e., permanent) populations in an open ecosystem, which are unlikely to be eliminated by man or natural causes.

Synonym: naturalized

Invasive Species:

1) A species that threatens the diversity or abundance of native species, the ecological stability of infested ecosystems, economic activities dependent on these ecosystems, and/or human health.

Synonyms: harmful, injurious, invader, noxious, nuisance, pest

2) Non-indigenous species whose introduction does or is likely to cause economic or environmental harm to human health (Executive Order 13112, Clinton 1999).

Current Regulatory Protections of *Zostera japonica* in Washington State

Discussion leader: Blain Reeves

Listed below are details from some of the state and federal regulatory protections that include *Zostera japonica*, in addition, WACs govern eelgrass protection via state laws (RCWs) and concern the rights of aquaculturists to property development (RCWs include 77.115.010, 77.12.047, 77.60.060, 77.60.080, 77.65.210, 77.115.030, & 77.115.040).

Hydraulic Code Rules WAC 220-110-250 Saltwater habitats of special concern

- Eelgrass (*Zostera* spp. [includes all species from the genus *Zostera*])
- Kelp (Order Laminariales)
- Intertidal wetland vascular plants (except noxious weeds)
- Eelgrass and vegetation that provides settlement and nursery areas for Pacific herring, rockfish, lingcod and juvenile salmonids

Shoreline Management Act

Critical saltwater habitats include all kelp beds, eelgrass beds, spawning and holding areas for forage fish, such as herring, smelt and sandlance; subsistence, commercial and recreational shellfish beds; mudflats, intertidal habitats with vascular plants, and areas with which priority species have a primary association. Critical saltwater habitats require a higher level of protection due to the important ecological functions they provide. Ecological functions of marine shorelands can affect the viability of critical saltwater habitats. Therefore, effective protection and restoration of critical saltwater habitats should integrate management of shorelands as well as submerged areas. See: WAC 173-26-221 (2.C iii and iv).

WAC 173-26-221 Regulatory protections - General master program provisions

“Critical saltwater habitats include all kelp beds, eelgrass beds... mudflats, intertidal habitats with vascular plants.”

Growth Management Act and Fish and Wildlife Habitat Conservation Areas

The GMA requires cities and counties across the state to address land use issues that directly and indirectly impact fish and wildlife habitat. Fish and wildlife habitat conservation is the management of land for maintaining species in suitable habitats within their natural geographic distribution so that isolated subpopulations are not created. This does not mean that all individuals of all species must be maintained at all times, but it does mean cooperative and coordinated land use planning is critically important among counties and cities in a region. In some cases, intergovernmental cooperation and coordination may show that it is sufficient to ensure that a species will

usually be found in counties and cities in a region. The designation of fish and wildlife habitat conservation areas should include:

Areas with which endangered, threatened, and sensitive species have a primary association.

- Habitats and species of local importance.
- Commercial and recreational shellfish areas.
- Kelp and eelgrass beds.
- Mudflats and marshes.
- Herring, surf smelt and sand lance spawning areas.
- Naturally occurring ponds under 20 acres and their submerged aquatic beds that provide fish or wildlife habitat.
- Waters of the state.
- Lakes, ponds, streams, and rivers planted with game fish by a governmental or tribal entity.
- State natural area preserves and natural resource conservation areas.
- Areas critical for habitat connectivity.
- See <http://www.commerce.wa.gov/site/747/default.aspx>

Additional regulatory measures that include *Z. japonica* protection:

- Army Corps of Engineers, Seattle, Washington – Regional General Permit 6
- Army Corps of Engineers, Seattle, Washington – Regional General Permit 48
- Army Corps of Engineers - Nationwide Permit 48
- Critical Area Ordinance – Fish and wildlife habitat conservation areas
- Pacific Coast Groundfish Fishery Management Plan
 - Habitat Areas of Particular Concern (HAPC) 7.3
- WDFW Priority Habitats ‘Puget Sound Nearshore’ (WDFW 2010)

Discussion Structure

The goal of our discussions was to determine the status of research for *Zostera japonica* in the Pacific Northwest. We asked if *Z. japonica* was a serious threat to Washington States outer coasts and estuaries and Puget Sound. Here are guidelines that the organizers and participants used to help structure discussion during the *Z. japonica* workshop.

Things to consider:

- Are the effects of *Z. japonica* positive/negative/neutral?
- What are the short vs. long-term effects of *Z. japonica* (1, 5, 20, to ~100 years)?
- Are these real vs. perceived effects? Consider both the strength and quantity of data.
- How does *Z. japonica* affect the economy/ecology/recreation activities for estuaries it colonizes?
- What are the impacts of management/no management?
- Considering scale of impact, is there an abundance of *Z. japonica* that sustains positive impacts? How can it be removed to minimize negative impacts?
- How should/can impacts to structure/function be studied?
- How should/can ecological and economic value of estuarine organisms be balanced?

It is also important to consider what types and quantities of data are necessary to make decisions regarding the management of a non-native species.

- What are its biotic/abiotic impacts?
- Do small scale patterns reflect those seen on a landscape scale and vice versa?
 - Is there enough similarity in community interactions and physiology of *Z. japonica* among estuaries to make inferences transferable?
- Do we know the net environmental effects?

Session One: Potential Impact of *Zostera japonica* Establishment on Ecosystem Structure and Function

Discussion leaders: Megan Mach and Kim Patten

Seagrasses in general have the following effects on ecosystem functioning: they slow water flow, increase sedimentation of fine particles, increase organic material in sediments, and stabilize sediments. The finer particles lead to reduced diffusion of oxygen into sediments, but roots and rhizomes of seagrasses are surrounded by an oxygenated rhizosphere. Because they can take up nutrients from both the water column and sediment porewater, seagrasses potentially reduce nutrient pools in both habitats. Finally, seagrasses are a source of primary production. Tissue quality tends to be low relative to micro- and macro-algae, but seagrasses are consumed by some herbivores and also contribute to detrital-based food webs (reviewed in Hemminga and Duarte 2000).

For *Zostera japonica* in particular, only a small subset of these potential effects has been tested in Washington State. In some cases, conditions with *Z. japonica* have been compared to unvegetated tideflat, and in other cases to *Z. marina*.

Specific information about *Z. japonica*'s effects on ecosystem function are poorly documented, yet *Z. japonica* is both known and expected to alter abiotic properties of intertidal flats, particularly in comparison to unvegetated areas. In addition, based on the substrate, structure and biogeochemical cycling *Z. japonica* provides, it is similar to *Z. marina*'s function in an estuary. The decomposition rate of *Z. japonica* (1.65% of total mass lost per day) is significantly faster than *Z. marina* (1.35% of total mass lost per day) (Hahn 2003). Higher decomposition rate could be due to the smaller size of *Z. japonica*, thus a higher surface area to volume ratio; alternatively *Z. japonica* may be simply more labile than *Z. marina* and therefore decompose faster. This additional particulate and dissolved organic matter (POM; DOM) is then available for consumption by organisms such as zooplankton and filter feeders, however the effect of this additional material in the food chain has not been studied or modeled. Hahn (2003) found that microbial assemblage is strongly influenced by the type of associated vegetation and differs between *Z. marina* and *Z. japonica* communities. These differences could lead to differing rates of decomposition and nutrient retention; alter the interaction between the microbes and the vegetation and affect higher trophic levels.

While *Z. japonica* releases POM and DOM into estuaries, it also takes up nutrients. Nutrient uptake within a bed of *Z. japonica* is higher than on mudflats without *Z. japonica*, which has the potential to limit nitrogen levels in estuaries that are already nitrogen-limited (Larned 2003). However, another study by Tsai et al. (2010) showed that there were no differences in ammonium levels in porewater (water sampled from below ground) where *Z. japonica* was present vs. removed. Also, Kaldy (2006) showed extremely high levels of porewater ammonium in sediments occupied by *Z. japonica*, although a comparison to bare tideflat or *Z. marina* was not done. In Padilla Bay, Bulthuis and Margerum (2005) showed nitrogen in overlaying water was reduced by up to 90% during the summer as it passed through the eelgrass community, though this study included both *Z. marina* and *Z. japonica*. Conflicting evidence of nutrient use by *Z. japonica* makes a discussion about potential effects on nitrogen cycling difficult.

As an upright vegetative plant, *Z. japonica* slows water flow by up to 40% relative to unvegetated mudflat (Tsai et al. 2010). Changes in waterflow can affect how organisms use mudflats. For example, species requiring high water flow for respiration or filter feeding may have their survival affected by *Z. japonica*.

In Willapa Bay, *Z. japonica* is estimated to cover 7.7% of the bay's surface area and contribute 4.79×10^6 kg dry weight production annually. For comparison, *Z. marina* occupies 9.6% of area and contributes almost an order of magnitude more production (3.53×10^7 kg dry weight; Ruesink et al. 2006). *Z. japonica* contributes additional macrophyte production, because it has colonized previously unvegetated tideflat; however, no exploration has been carried out to determine whether this may come at the expense of production by benthic microalgae.

Research discussion points from ecosystem structure and function session:

Suggestions for research:

1. Comparative studies need to be done that involve multiple vegetated and unvegetated habitats: macroalgae, *Z. marina*, mudflat, etc.
2. The effect of *Z. japonica* on tide flat topography should be determined (bioengineering).
3. How do shifts in primary production effect communities in terms of nutrients and carbon cycling (particularly microalgae to microalgae)?
4. What is the effect of scale on experimental outcome (single site, single estuary, multiple estuaries, landscape)?
5. Models of potential food web effects of decreased nutrient levels, altered microbial assemblages and increased DOM/POM would help to predict and explain the effect of *Z. japonica* on the estuarine community.
6. What are the supporting ecosystem services associated with *Z. japonica* (supporting ecosystem services include but are not limited to nutrient uptake, filtration and carbon sequestration)?
7. How is time (1, 5, 10 years, short term or long term) considered when measuring the effects of *Z. japonica* within an estuary in terms of decreased nutrient levels or increased decomposition? These subtle effects may take many years to take effect in the ecosystem or they may happen so quickly that the impact will happen before management options can be considered.

Session Two: Community and Species Level Interactions involving *Zostera japonica*

Discussion leaders: Jennifer Ruesink and Michael Hannam

Interactions with Macrophytes

One of the key questions regarding *Zostera japonica*'s community interactions *in its non-native range* is its effect on the native eelgrass, *Z. marina*. Studies from the literature were discussed as the primary source of information for understanding these interactions. In most cases in the Pacific Northwest region, there is little opportunity for direct competition between the two *Zostera* species because they occupy different niches in the intertidal zone (Shafer 2007). Where they do overlap, neither species is clearly competitively dominant, since biomass and density of both species are reduced in the presence of the other.

Bando (2006) – Bando tested the effects of disturbance on plant recruitment by clearing plots in the *Z. japonica* and *Z. marina* mixed tidal zones and measuring plant recolonization back into the plots. *Z. japonica* recruited in first, and over the two years of the study, *Z. marina* never moved back into the cleared plots. Bando also tested competition between *Z. japonica* and *Z. marina* however there is some confusion within the paper regarding their respective growth rates. In the text Bando states that *Z. marina* grows most quickly in non-mixed plots, and more slowly when mixed with *Z. japonica*. However Fig. 1 shows the opposite trend with *Z. marina* growing more quickly in mixed plots, and more slowly when in monospecific stands. In addition this study was done at only one site in Willapa Bay, WA, in shallow pools at +1-2 m MLLW, as such, results may not apply to areas where *Z. japonica* and *Z. marina* are exposed at low tides.

Hahn (2003) – Hahn transplanted *Z. japonica* sods in to all three zones and reciprocal transplants back into those zones but primarily measured responses in terms of microbial abundance and functional diversity.

Harrison (1982) – Harrison demonstrated in a laboratory study that in cool temperatures and high light, leaf elongation (recorded as cm of growth per shoot) occurred in *Z. japonica* at the same rate as *Z. marina*. Workshop participants discussed the validity of this argument, because the blade architecture of *Z. marina* is much broader than *Z. japonica*, it may therefore be more productive for each cm of growth. The two species were not grown together to test for competitive effects

Nomme and Harrison (1991a) – A multivariate test of the density of *Z. marina* and *Z. japonica* based on observed densities in the high *Z. japonica*, mixed, and low *Z. marina* tidal zones is described in this study. The authors found *Z. japonica* density was lower in the mixed zone, but *Z. marina* density was not significantly affected by tidal zone. Additionally, the study showed that morphology of each species varied by tidal zone.

Nomme and Harrison (1991b) – To test if competition, not light, temperature, or other physical factors limits growth of *Z. japonica* in the lower elevations, Nomme and Harrison transplanted *Z. japonica* and *Z. marina* into three tidal zones: the high *Z. japonica* zone (+2 to +3m), the mixed species “transition” zone (+1 to +2m), and the lower *Z. marina* zone (+1 to -1 m). Shoot counts

did not show a consistent effect of depth on the density of either species. The authors dismissed the effect of depth and asserted that competition reduced shoot growth of *Z. japonica*. However, the *Z. japonica* transplants had lower shoot growth in all but one transplant in the lower *Z. marina* zone, which would suggest there was an effect of depth on density.

Ruesink et al. (2010) – In Willapa Bay, permanent transects at 14 locations were sampled at two time points, four years apart. The authors found *Z. marina* moved upshore into *Z. japonica* zones and suggested that this is caused by *Z. japonica* retaining water, thus physically altering the upper intertidal zone to mimic a lower tidal elevation. However, the study is based on two time points, and studies over a longer period of time may have yielded different results.

Interactions with Benthic Invertebrates

Zostera japonica is expanding into what had likely been unvegetated tidal flat, adding a complex structure of rhizomes and leaf blades. Introduced macrophytes often have negative competitive effects on other infaunal space occupiers, as well as epifauna, in comparison to native macrophytes (Thomsen et al. 2009). In contrast, other studies of invasive macrophytes document higher diversity and abundance of associated organisms relative to unvegetated areas (Posey 1988, generally Crooks 2002, Neira et al. 2005, McKinnon et al. 2009). Past studies have described structure forming species invasions as having a positive impact on small benthic infauna through facilitation by the new complex structure, while the added structure would result in increased competition with larger organisms. Interactions between *Z. japonica* and benthic macrofauna demonstrate both negative and positive effects to macrofauna, though the limited number of studies prevents a definitive assessment of patterns (described below; Figure 3).

Berkenbusch et al. (2007) – Berkenbush et al. addressed the interaction of burrowing ghost shrimp (*Neotrypaea californiensis*) and *Z. japonica* by conducting transplants in the field and altering density of *Z. japonica* and numbers of ghost shrimp. The authors state that ghost shrimp burrow numbers were reduced in the presence of *Z. japonica* but only weak interaction effects support this claim. The study took place in the summer over four and half months.

Dumbauld and Wyllie-Echeverria (2003) – The influence of burrowing ghost shrimp (*Neotrypaea californiensis*) on the distribution of *Z. japonica* was studied by applying the pesticide carbaryl to control shrimp populations. Oyster aquaculturists in Willapa Bay, WA commonly use carbaryl to reduce densities of ghost shrimp. Dumbauld and Wyllie-Echeverria found that, when the mudflat is sprayed with carbaryl, ghost shrimp densities were reduced but the *Z. japonica* densities increased. *Z. japonica* appeared to form slightly raised areas of sediment where the carbaryl was sprayed (Figure 2) although this feature was not discussed in the study.

Harrison (1987) – The densities of burrowing shrimp (*Callinassa [Neotrypaea] californiensis*), *Z. marina*, and *Z. japonica* were tracked after large causeways were built in Roberts Bank, BC. As vegetation density increased, burrow densities decreased. A bioturbator, such as the burrowing shrimp, is likely limited by the increased underground *Zostera* spp. rhizome structure. However, Figure 5 in this paper suggests the burrows may have been already declining. An additional experiment showed removal of all shoots allowed adult shrimp to colonize the sediment while addition of *Z. japonica* shoots caused a temporary decrease in shrimp abundance.

However, after a few weeks, the shrimp destroyed the plant transplants by disturbing below-ground structures.

Posey (1988) – Cores were extracted and measured for abundance and richness of infaunal species in *Z. japonica* patches and unvegetated mudflats. Infaunal species richness and density were higher in *Z. japonica* cores than in those from the mudflats without rooted vegetation.

Tsai et al. (2010) – Tsai et al. examined the effect of Manila clam density (*Ruditapes philippinarum*) and *Z. japonica* on clam size, weight, and recruitment of clams. They found a reduction of clam condition (weight of dry meat per clam) in *Z. japonica* plots vs. removed or harrowed *Z. japonica* sites, with no effect on clam shell growth or recruitment. They also found that *Z. japonica* grew faster when transplanted into vegetated plots than into removal plots, suggesting some facilitation of its own growth in intertidal zones.



Figure 2: The effects of carbaryl sprayed onto the intertidal sediment in strips to control burrowing shrimp resulted in a distinct pattern in *Z. japonica* distribution one year after pesticide application (Dumbauld and Wyllie-Echeverria 2003).

Interactions with Megafauna

Megafauna, such as fish and migratory waterfowl, utilize seagrasses for food and habitat, though few studies have focused on *Z. japonica*.

Baldwin and Lovvorn (1994) – In Boundary Bay (on the Washington/British Columbia border), up to 84% of the diet of migrating waterfowl consists of *Z. japonica*. *Z. japonica* increases seagrass biomass in the mid to upper intertidal by 2161 ha, adding millions of bird use days to Boundary Bay. They also found *Z. japonica* to have a higher leaf caloric content than *Z. marina*.

Lovvorn and Baldwin (1996) – Biomass of *Z. japonica* in Boundary Bay was insufficient to support American wigeon (*Anas americana*) through the winter. These birds move into nearby farmland to find additional food sources.

Semmens (2008) – In Willapa Bay juvenile Chinook salmon slow their swimming speeds in *Z. marina* but do not prefer or avoid *Z. japonica*. It is possible, however, that the salmon in this study were too large and mature to adequately utilize the vegetation, although they were sourced from a hatchery just prior to smolt release. A preference for associating with the net enclosure was removed statistically prior to assessing behavior across patches of habitat. It would be useful to perform other studies involving different species and sizes of salmon (and other fish) before drawing firm conclusions about *Z. japonica* as habitat.

Simenstad (1994) – Simenstad described an indirect negative relationship of *Z. japonica* on economically and ecologically important fish species: surf smelt, Pacific herring, Pacific sand lance, and chum salmon. This relationship was predicted as result of reduced copepod biomass in *Z. japonica* (Simenstad et al. 1988), these fish are reliant on the copepods as a food source.

Thom et al. (1995) – Thom et al. demonstrated that seagrass beds in Padilla Bay are functionally similar for epibenthic organisms, they found populations of invertebrate grazers in *Z. japonica* to be similar to those found in *Z. marina*.

Research discussion points from community interaction session:

It is difficult to assess *Z. japonica*'s effect on community interactions when some species are using *Z. japonica* as food or habitat, some species are negatively affected in density or performance, and some do not respond at all. This complicates an assessment of the overall impact of *Z. japonica* since whether it is harmful or beneficial may depend on which species is of concern (Figure 3). Native species have not previously experienced seagrass at the tidal elevation occupied by *Z. japonica*, but, in other cases such as threatened waterfowl utilizing invasive plants (Hershner and Havens 2008) and birds finding habitat in invasive tamarisk in the arid southwest (Zavaleta 2000), native species can come to depend on non-natives for habitat. A key component of understanding *Z. japonica* impact is an assessment of whether it is providing novel vegetated habitat at mid-intertidal elevations and whether it functionally replaces *Z. marina* at lower tidal elevations.

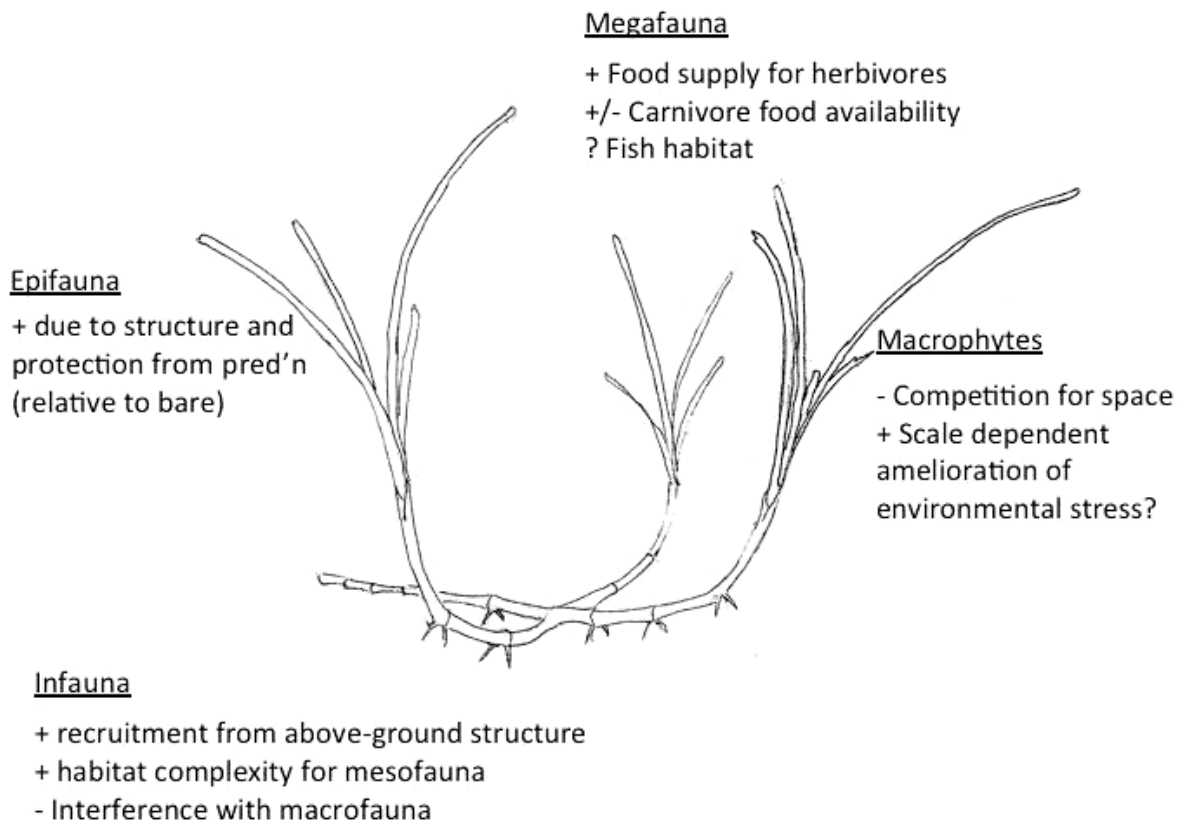


Figure 3: Diagram of *Z. japonica*'s community interactions, +/- suggests a change in biomass according to previous studies (from Ruesink & Hannam's workshop presentation; drawing by M. Hannam).

Conclusions from discussion:

Suggestions for methods:

1. Replicated studies must take place over broader geographic areas.
2. Studies should stratified by different zonation patterns of *Z. japonica* (Shafer 2007).
3. Comparative studies that involve multiple habitats (*Zostera* spp., macroalgae, and unvegetated mudflats) should be executed to compare *Z. japonica* both to unvegetated areas and to other types of vegetation that may occur at a similar tidal elevation (although these are rare).
4. Refer to methodologies that established *Z. marina* as essential habitat and apply these methods and experimental designs to the investigation of *Z. japonica* community structure (Short and Coles 2001).

Suggestions for research:

1. It is important to understand how *Z. japonica* is utilized by commercial and recreational fisheries species, waterfowl, migratory shorebirds, and wading birds.
2. Consequences of *Z. japonica* for the population dynamics of all species found in *Z. japonica* beds should be characterized.
3. Carbon isotope analysis should be used to distinguish food sources (*Zostera* spp., macroalgae, etc) for estuarine invertebrates and how that carbon moves through trophic levels to megafauna. How does this carbon source differ in *Z. japonica* dominated areas?
4. Studies should determine interactions between infauna (especially ghost shrimp), epifauna, shellfish and *Z. japonica*.
5. How does *Z. japonica* interact with the estuarine community in its native range? How do similar species to *Z. japonica*, such as *Z. noltii* interact with their estuarine communities?
6. Diversity and abundance of invertebrates in *Z. japonica* beds should be assessed, and compared to that of unvegetated mudflats.
7. Use or avoidance of *Z. japonica* by endangered species (e.g., Green Sturgeon in Willapa Bay) should be studied.
8. Interaction between *Z. japonica* and other macrophytes, especially *Z. marina*. Are they competing?
9. The ecological and economic impacts of mudflat vs. *Z. japonica* vs. aquaculture species vs. both together as a mosaic (at Willapa Bay and other sites) should be studied.
10. Can *Z. japonica* and aquaculture species (and aquaculture practices/techniques) coexist?
11. What are the regulatory ecosystem services, such as habitat and nursery grounds, provided by the presence of *Z. japonica* that benefit or negatively affect the estuarine community?
12. What is the economic value of *Z. japonica* net gain or loss? What is the value of *Z. japonica* ecosystem services?

Session Three: Monitoring *Zostera japonica* Distribution and Expansion

Discussion leaders: Jeffrey Gaeckle and Douglas Bulthuis

Understanding *Zostera japonica*'s distribution and potential for expansion in the Pacific Northwest is essential to establish a research context.

Tidal Zonation

Zonation patterns of co-occurrence between *Z. japonica* and the native seagrass *Z. marina* were originally described by Shafer (2007) as:

- 1) Disjunct distribution – *Z. japonica* only in the high tidal zone, no vegetation in mid tidal zone, *Z. marina* only in the low tidal zone– steep topography [70% of sites]
- 2) Overlapping distribution – *Z. japonica* only in the high tidal zone, mix of *Z. japonica* and *Z. marina* in the mid tidal zone, *Z. marina* only in the low tidal zone – flat topography [30% of sites]
- 3) Mosaic distribution – A variation of the overlapping distribution pattern. *Z. japonica* only in the high tidal zone, patchy mid tidal zone with *Z. marina* in a dominantly *Z. japonica* zone or the opposite (with pronounced microtopography), *Z. marina* only in the low tidal zone [2 or 3 sites]

These patterns likely result from wave energy and shoreline slope, which could control the vertical distribution of *Z. japonica* (Shafer 2007). There is evidence that the lower edge of *Z. japonica* tidal distribution is not variable, and it is variation in *Z. marina*'s upshore tidal limit that causes the patterns of co-occurrence described above (Britton-Simmons et al. 2010).

Estuary Distribution

Mapping in Willapa Bay and Grays Harbor

In 1982 Harrison and Bigley (1982) mapped the occurrence of *Z. japonica* in Willapa Bay and Grays Harbor. From beach based surveys they documented 17,000 ha of *Z. japonica* on intertidal flats and called the *Z. japonica* beds in Willapa Bay the most extensive in North America.

From 1975 to 1977 Miller (1977) measured a 518% increase in *Z. noltii* (now *Z. japonica*) in Grays Harbor from 680 to 4210 acres, though there is little information about its density and abundance across this area.

Mapping in Padilla Bay

The first introduction of *Z. japonica* from Japan into Padilla Bay likely occurred when oyster culture began in the 1930s (Figure 6).

The earliest hydrographic surveys done in Padilla Bay only recorded depth and, in some cases, refer to “GR” if grass (*Zostera* spp.) was brought up in the sample. The hydrographic survey in

Padilla Bay was also done in two pulses: a northern survey and, ten years later a southern survey. It is impossible to know if the data in these two surveys were gathered with the same accuracy (information from workshop, D. Bulthuis).

Eelgrass has been mapped in Padilla Bay since 1989 (Bulthuis 1995). Through aerial mapping and groundtruthing, time series distributional maps have been created. Between 1989 and 2000 *Z. japonica* expanded mainly into bare mudflats and somewhat into *Z. marina* habitat in the eastern and northeastern regions of the bay (Figure 4, Shull and Bulthuis 2002). In southern regions *Z. marina* expanded onto previously bare intertidal flats (Shull and Bulthuis 2002). The 2004 aerial mapping measured a slight increase in *Z. marina* from 2000 and a large decrease in *Z. japonica*. From 2000 to 2004 the estimated distribution of *Z. japonica* decreased from about 835 hectares to about 475 hectares (Table 1). However, the extent of these various changes in distribution are not easily quantifiable because classification categories differed among surveys and extent of groundtruthing varied among surveys. In addition, it can be difficult to accurately distinguish between the two *Zostera* species in aerial photographs without extensive groundtruth investigation.

In 2002, monitoring by the Submerged Vegetation Monitoring Project (SVMP; Department of Natural Resources) observed 610 ha of *Z. japonica* in Padilla Bay. In 2009, the SVMP observed 890 ha of *Z. japonica*. These data are strictly preliminary and should not be used to suggest an increase over time as the focus of the SVMP is to monitor *Z. marina* and the methods are currently unable to sample the entire extent of the *Z. japonica* potential habitat. This effort also determined that *Z. japonica* grows between -0.5 and +0.8 meters MLLW. Again, the observed upper extent is likely not accurate due to methodological limitation.

Table 1: Preliminary data assessment of change in spatial extent of *Z. marina* and *Z. japonica* based on aerial photographs in Padilla Bay (D. Bulthuis and S. Shull, unpublished data). Size of total extent in hectares is estimated in 1989, 2000, and 2004.

Seagrass Species	1989	2000	2004
<i>Z. marina</i>	2884	3030	3140
<i>Z. japonica</i>	236	836	476

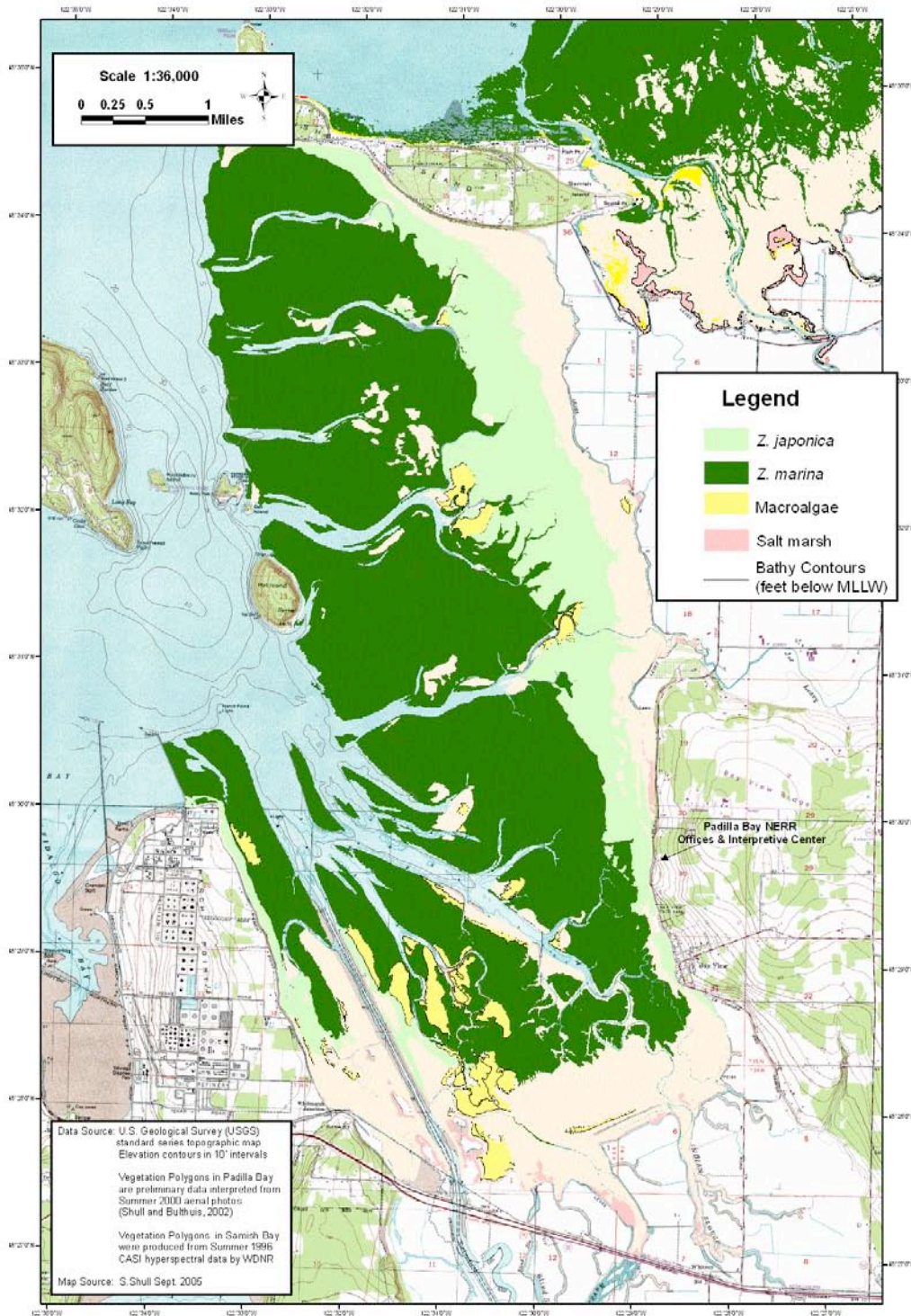


Figure 4: Map of the special extent of *Z. marina* and *Z. japonica* extent in Padilla Bay, WA during the summer of 2000 (Shull and Bulthuis 2002).

Eelgrass population monitoring in Puget Sound

The Submerged Vegetation Monitoring Project (SVMP; Department of Natural Resources) has monitored *Z. marina* status and trends in Puget Sound over the last 10 years. In the process of collecting *Z. marina* data, field efforts also record the presence of *Z. japonica* at the lower edge of its tidal range. These data are collected using underwater video from an 11m research vessel (Norris et al. 1997, Berry et al. 2003; DNR website), so monitoring could potentially miss exposed portions of *Z. japonica*'s high tidal range. The vessel performs random transects perpendicular to shore at an approximate speed of 1 meter/second. A scientist records seagrass presence/absence aboard the research vessel and the data is further reviewed in the lab to increase precision and species identification. The resulting transect data are plotted spatially to show the presence and absence of *Z. marina* and *Z. japonica*. These data are used to extrapolate total area at the randomly selected sites sampled through the greater Puget Sound (Berry et al. 2003, Dowty et al. 2005, Gaeckle et al. 2007, Gaeckle et al. 2008, Gaeckle et al. 2009). To date the SVMP has sampled 378 sites in the greater Puget Sound (waters east of Cape Flattery and south of the Canadian border), and *Z. japonica* has been identified at 68 of those sites (Figure 5).

Some concerns with this monitoring program include the lack of a complete sampling of Puget Sound coastline (since sampling locations are chosen randomly based on a probabilistic random sample design), the shallowest edge of *Z. japonica* is not captured because of restricted water depth for the research vessel, and anecdotal observations are not captured as part of the program.

Additional anecdotal distribution information for *Z. japonica* locations in Puget Sound provided by conference participants, likely present at many other sites in the greater Puget Sound:

- Dickenson Cove
- Tolmie State Park
- Echo Bay, Sucia Island
- Griffin Bay
- Northwest Side of Vashon Island
- Alki Beach (West Seattle)
- Max Welton Beach, Whidbey Island

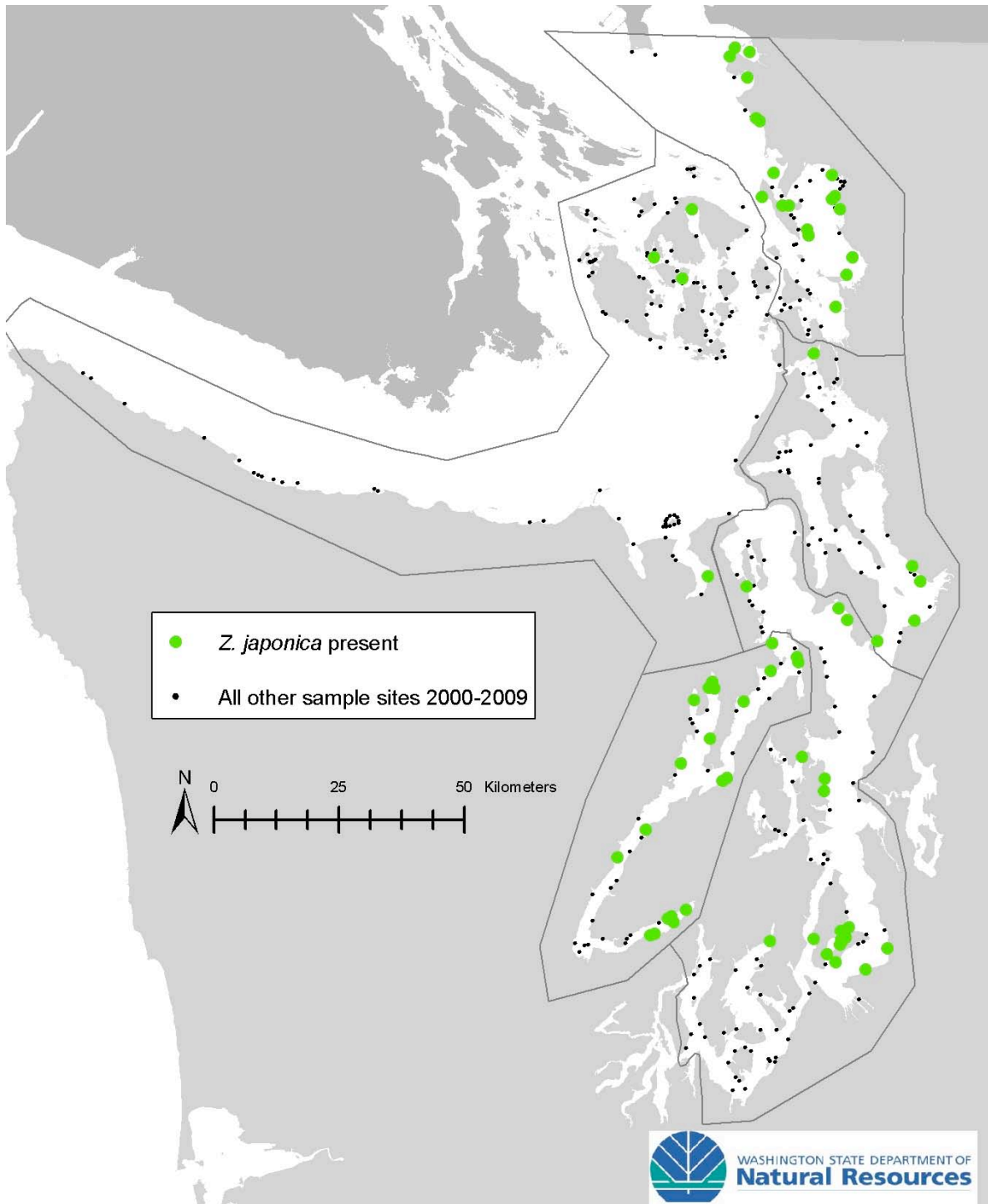


Figure 5: Sites where *Z. japonica* was observed in Puget Sound between 2000-2008 (Gaeckle et al. 2009).

Zostera japonica Range and Distribution

The northern extent of *Z. japonica* distribution is currently documented as English Bay on the BC mainland and Campbell River on Vancouver Island (Table 2), however, its current northern extent into the Strait of Georgia is undocumented and likely extends further north than these locations. In addition, there are no recorded sightings of *Z. japonica* on the outer coast of Vancouver Island. *Z. japonica*'s southern extent, which is more intensely monitored, currently extends to Humboldt, CA (Table 2).

Table 2: Location of currently known *Z. japonica* populations in the Pacific Northwest region (modified from Shafer 2007).

Location	Reference	Position
British Columbia		
English Bay, Vancouver	Harrison and Bigley 1982	
Sturgeon Bank (Fraser River Delta)	Harrison and Bigley 1982	
Roberts Bank (Fraser River Delta)	Harrison and Bigley 1982	49° 30.0, 123° 6.0
Boundary Bay	Harrison and Bigley 1982	
Nanaimo (Vancouver Island)	Harrison and Bigley 1982	
Semiahoo Bay	Harrison and Bigley 1982	
Near public wharf, Fernwood, Salt Spring Island	Chris Tanner ¹ , pers. obs., July 2008	48° 54.956, 123° 31.985
Southey Point, N end of Salt Spring Island	Chris Tanner ¹ , pers. obs., July 2008	48° 56.541, 123° 35.858
S of Campbell River, Vancouver Island	Chris Tanner ¹ , pers. obs., July 2008	49° 53.725, 125° 08.566
N end of Protection Island in Nanaimo Harbor	Chris Tanner ¹ , pers. obs., July 2008	49° 10.989, 123° 55.406
Washington		
Birch Bay	Harrison and Bigley 1982	
Bellingham Bay	Harrison and Bigley 1982	
Chuckanut Bay	Harrison and Bigley 1982	48° 40.2, 122° 30.0
Samish Bay	Harrison and Bigley 1982	
Padilla Bay	Harrison and Bigley 1982	
Indian Cove, Shaw Island	Shafer 2007	
Max Welton Beach, Whidbey Island	Shafer 2007	
Dumas Bay, Puget Sound	Shafer 2007	
Hood Canal, Puget Sound	Harrison and Bigley 1982	

Table 2 continued

Location	Reference	Position
Grays Harbor	Miller 1977; Harrison and Bigley 1982; Phillips 1984; Thom 1984 (<i>Z. noltii</i>)	
Willapa Bay	Harrison and Bigley 1982; Phillips 1984	
Oregon		
Netarts Bay	Harrison and Bigley 1982; Phillips 1984; www.wa.gov/durin_sound/shared/nis.html	
Yaquina Bay	Kaldy 2003; Shafer 2007; Shafer et al. 2008	
Coos Bay South Slough Day Creek Inlet	Harrison and Bigley 1982; Phillips 1984; Posey 1988; Shafer 2007, Shafer and Kaldy 2010	
Coquille Bay	www.wa.gov/durin_sound/shared/nis.html	
Siletz Bay	www.wa.gov/durin_sound/shared/nis.html	
Salmon River estuary	www.wa.gov/durin_sound/shared/nis.html	
Tillamook River estuary	www.wa.gov/durin_sound/shared/nis.html	
Nehalem	www.wa.gov/durin_sound/shared/nis.html	
Young's Bay	www.wa.gov/durin_sound/shared/nis.html	
California		
Humboldt Bay	CA Sea Grant, Sept 2001 (Susan Schlosser ² , unpublished data)	

¹Christopher E. Tanner, Marine and Estuarine Ecologist, St. Mary's College of Maryland, St. Mary's City, MD

²Susan Schlosser, Marine Advisor - Humboldt and Mendocino Counties, California Sea Grant, Eureka, CA

Research discussion points from distribution and monitoring session:

Is it important to continue monitoring *Z. japonica* in Washington State? With a large and continuous set of data we will be able to understand overall trends and fluctuations in species distribution with time. With these data it might be possible to trace the effects of El Niño/La Niña cycles and regime shifts on seagrass abundance and distribution patterns.

Parameters for continued monitoring:

- Geographical distribution and abundance
- In addition to Padilla and Willapa Bays, delineate distribution and abundance within other bays and coastal estuaries and update dated abundance information (e.g. Grays Harbor)

- Determination of upper and lower depth limits
- Distribution relative to *Z. marina* (e.g. zonation patterns *sensu* Shafer 2007)
- Status and trends of above parameters

Conclusions from discussion

Suggestions for research:

1. How do interaction between *Z. japonica* and other macrophytes limit vertical tidal distribution?
2. SVMP dataset should be mined for additional data, such as site specific areal extent and upper and lower depth distribution, to test null hypothesis that maximum depth of *Z. japonica* is relatively constant.
3. Bays in Washington State should be monitored for change in distribution over time to determine population dynamism.
4. Methods should be developed for tracking and verifying anecdotal reports of *Z. japonica*.
5. Develop and verify models to predict changes in *Z. japonica* populations (this has been done in Yaquina Bay, Oregon (Almasi and Eldridge 2008)).
6. What environmental factors control *Z. japonica* morphology and demography?
7. What are *Z. japonica*'s distribution and species interactions in native range (literature review)?
8. Are there any studies in the established or native range that demonstrate how growth of *Z. japonica* varies across the tidal depth range (e.g., *Z. marina* grows differently in the high intertidal vs. the shallow subtidal)?
9. How does *Z. japonica* expansion occur (seeds, waves and currents, birds, vegetative fragments, people, etc.)?
10. Predictive models should be developed to estimate what intertidal flats in Washington are at risk of colonization by *Z. japonica*.
11. Studies need to take place over broader geographic areas, with replication, to document changes in biogeographic range over time.

Session Four: Influence of Predicted Climate Change on *Zostera japonica* Distribution

Discussion leaders: Deborah Shafer and James Kaldy

Global climate change (GCC) in coastal estuaries

Understanding *Zostera japonica*'s physiological responses to global climate change (GCC) is important for predicting future distribution and abundance patterns. This information is also necessary for predicting the outcome of increased competitive interactions with the native eelgrass, *Z. marina* and other estuarine organisms. Studies have shown that seagrass abundance and flowering may be influenced by current El Niño/La Niña patterns (Nelson 1997, Short and Neckles 1999, Johnson et al. 2003, Echavarría-Heras et al. 2006, Shafer et al. 2008). The magnitude of GCC in the Pacific Northwest region and its effects on regime shifts in the Pacific Ocean may also influence *Z. japonica*'s spread and future distribution in the eastern North Pacific. A more complete suite of studies on *Z. japonica*'s physiological tolerances is needed before it will be possible to accurately predict the effect of GCC on the spread and ecosystem impact of *Z. japonica*.

Expected changes in Puget Sound and along the open coast

Effects of GCC in Puget Sound and on the open Pacific coastline have the potential to alter species ranges, change phenological patterns of these species, and greatly affect local biodiversity. Snover et al. (2005) outlined the magnitude and direction of these expected changes for Puget Sound, which can be modified to include the more exposed outer coast of Washington. It should be noted that all of these potential changes will likely occur at the same time, thus interactions and potential synergisms are also expected.

- Increase in erosion – Sea level rise and an increase in storms are likely to increase the rate and extent of erosion and loss of nearshore habitats.
- Increased air temperature – Air temperatures are predicted to increase significantly more than the temperature increase already experienced over the last 100 years.
- Increased flooding – Rain is predicted to replace snowfall in the winter; increased precipitation is likely to result in flooding.
- Loss of wetlands and salt marshes – Sea level rise, temperature and nutrient fluctuations may cause further declines in critical coastal habitats
- Increase storm intensity and change in Pacific Decadal Oscillation (PDO) – Storms are predicted to increase with GCC and may be exacerbated by the PDO, which could result in increased erosion and flooding, especially on the open coast. Changes in the PDO can result in temperature and seasonal shifts, which may impact marine species that rely on seasonal cues for growth and reproduction.
- Change upwelling patterns – GCC is predicted to alter atmospheric circulation and local winds, potentially changing the strength and timing of coastal upwelling. Increased

upwelling intensification and timing could which will likely effect delivery of high nutrient, low dissolved oxygen water to estuaries.

- Water quality:
 - Change in dissolved oxygen – Increased algal productivity in surface waters would drive down oxygen levels in deeper waters as would higher water temperatures and stratification of the water column predicted with GCC.
 - Nutrients – Increased runoff may result in more nutrients entering Washington State waters, however the overall change will hinge on a balance of freshwater inflow, anthropogenic activities, biological productivity and changes in sea level.
 - Salinity – Salinity levels in Washington State, both on the outer coast and in Puget Sound are influenced by circulation patterns and salinity levels in the Pacific Ocean and the amount of freshwater inflow from snowmelt and rainfall. Records of historical salinity levels have not been tracked, making it difficult to predict future changes.
 - Continued temperature increases: Primary producers, such as plankton, are sensitive to water temperature change. Impacts from these temperature driven shifts could affect higher levels of the food web changing community dynamics.
- Increased carbon dioxide (ocean acidification) – decreased carbonate and increased ocean may impact organisms that use calcite to form their shells. These organisms range from plankton, such as coccolithophores, to mussels and crabs. Increased CO₂ availability may ameliorate carbon limitation for aquatic macrophytes.
- In Puget Sound, but not open coast estuaries:
 - Decrease in snowpack, earlier stream melt and low summer streamflow: Alters timing of freshwater flow into Puget Sound
 - Circulation – Circulation in Puget Sound is driven by coastal upwelling and salinity influence from the Pacific Ocean and its interaction with freshwater and temperature. The effects of circulation change on the biota are not well studied but decreases in circulation in areas such as Hood Canal could result in increased periods of hypoxia and anoxia in these oxygen-limited regions.
 - Potential density stratification will alter nutrient supply to surface water, dissolved oxygen levels at depth and pollution flushing. Stratification is likely to be the strongest in the winter with increases in stream flow.

Predicting *Z. japonica*'s response to GCC

Euryhaline species like *Z. japonica*, are well adapted to fluctuations in salinity and temperature, and the thermal tolerances of *Z. japonica* exceed those of *Z. marina* (Shafer et al. 2007). This suggests that *Z. japonica* may be well suited for predicted changes associated with GCC, and is likely to fare better than Washington's native eelgrass. In addition, southern populations of *Z. japonica* perform better under warmer temperatures (Shafer et al. 2007). Plants grow faster, have a higher P_{\max} , and have lower rates of respiration, which suggests these populations are more ecologically fit than northern populations (Shafer et al. 2008, Shafer et al. *In review*). Increased CO_2 levels predicted under GCC are likely to increase growth in *Z. japonica* and most vascular plants, algae, and plankton.

Physiological data and knowledge of its native latitudinal range (in the western Pacific, ~ N 20° to N 50°) suggest the southern limit of *Z. japonica* could be much farther south than its current extent (~N 40° to N 49°) (Shafer 2007). In addition, Shafer et al. (2008) tested temperature effects on growth and production of *Z. japonica* in its North American range, and showed southern populations were better adapted to high temperatures than northern populations, suggesting that further southward expansion of this species along the California coast is likely. As populations of *Z. japonica* continue to expand southward along the California coast, zonation patterns are likely to be affected by two factors: 1) the upper boundary may be shifted lower in the intertidal zone by increased desiccation associated with hotter and drier climate conditions, and 2) cold water temperatures and interspecific competition may limit expansion of the lower boundary into the lower intertidal and shallow subtidal zones (Shafer et al. 2008).

Preliminary photosynthetic data indicates that *Z. japonica* may utilize light more efficiently than *Z. marina* (J. Kaldy, unpublished data). If this preliminary trend is substantiated with additional analysis, this would suggest that *Z. japonica* is physiologically capable of growing at least as deep as *Z. marina*, if not deeper. This then, suggests that the vertical distribution of *Z. japonica* in the PNW could be controlled by a factor other than light, such as temperature or wave energy. *Z. japonica* appears to exhibit optimal photosynthesis and growth at temperatures above about 20 °C (Shafer et al. 2007, Shafer et al. *In review*). Likewise, experimental manipulations indicate that *Z. japonica* has a lethal temperature threshold of 35 °C (Kaldy and Shafer *Submitted*). Consequently, we hypothesize that *Z. japonica* vertical distribution may be confined to the upper intertidal by cold temperatures. Additionally, we hypothesize that *Z. japonica* will continue to spread latitudinally, until it is further constrained by extreme warm temperature to the south and colder temperatures to the north. This hypothesis is consistent with the findings of physiological research conducted in Japan (Abe et al. 2009b, a).

Overall, *Z. japonica*'s response to predicted climatic changes in Puget Sound and the outer coast of Washington is likely to be either a neutral change or an increase in biomass (Table 3).

Table 3: Hypothesized response of *Z. japonica* to GCC in Washington State. A. Factors in the environment that are likely to change in the Washington State during GCC and the resulting impact. B. Abiotic changes in the environment likely to be affected by GCC are “Variable” and have a physiological effect on *Z. japonica*.

A. Factor	PS	OC	Impact	<i>Zj</i> response
Sea Level Rise	+	+	decreasing light	↑
Storms	+	+	light, physical damage	↓
Upwelling	+	+	temperature, salinity, nutrients, decrease light	↑↓

B. Variable	Mechanism of Effect			
Air temp	+	+	Q ₁₀ physiology	↑
Water Temp	+	±	Q ₁₀ physiology	↑
Salinity	±	±	physiology	↑↓
Nutrients	±	±	eutrophication, competition	↑↓
CO ₂	-	-	alleviate Carbon limitation	↑

PS = Predicted increase or decrease of the factor in Puget Sound, OC = Predicted increase or decrease of the factor on the outer coast of Washington, *Zj* response = Hypothetical response, increase or decrease in biomass, predicted for *Z. japonica*. “↑↓” indicates that the response may be site specific.

Research discussion points from climate change session:

Suggestions for research:

1. What mechanisms limit the lower vertical range of *Z. japonica*? Specifically, is *Z. japonica* cold water limited?
2. Dispersal mechanisms
 - a. What are mechanisms for and limitations to dispersal?
 - b. What effects will dispersal have on range expansion and contraction after GCC?
 - c. What controls the timing and triggering of sexual vs. clonal reproduction.
3. Is *Z. japonica* susceptible to chemical changes caused by GCC (potential for mediating impacts of GCC or eutrophication)?
4. What are the effects of disease outbreak caused by GCC elements on *Z. japonica*?
5. What are the impacts of *Z. japonica* loss due to GCC or management?
6. What are the shifting competitive interactions between *Z. marina* and *Z. japonica*?

7. What is the potential for habitat replacement/shift due to rising and temperature stress on *Z. marina* and potential increase in *Z. japonica* with GCC?
8. What are the impacts of GCC on phenology and reproductive biology (i.e., timing and development of flowers and seeds)?
9. Genetic data should be gathered to complement physiological studies on potential for expansion under GCC.

Session Five: Non-native Status and Genetic Variation within and among *Zostera japonica* Populations

Discussion leaders: Richard Bigley and Jennifer Rhode Ward

Zostera japonica might have been introduced to the Pacific Northwest as packing material for Pacific oyster (*Crassostrea gigas*) seed (Harrison and Bigley 1982) to Willapa Bay and Samish Bay, WA. Pacific oysters were first documented in Washington in the 1920s, with importation tailing off in the 1970s (Figure 6). This suggests that *Z. japonica* might have been introduced in the early 1900s.

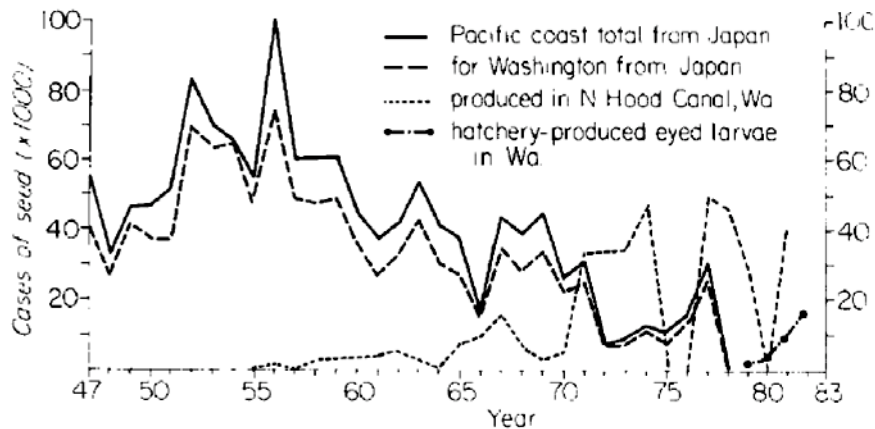


Figure 6: Total cases of Pacific oyster seed from Japan for the Pacific coast; cases from Japan planted in the state of Washington; equivalent cases produced in Hood Canal, Washington; and equivalent cases using hatchery-produced eyed larvae in Washington (Chew 1984).

In the 1980s *Z. japonica* rapidly expanded from Willapa Bay to Oregon estuaries. It also expanded both south and north from Samish Bay into the rest of Puget Sound and British Columbia, respectively. The rapid expansion of *Z. japonica* and its correlation to oyster seed importation has been used to argue that this is a non-native species (Sakai et al. 2001).

The use of genetics may provide insight into the role of *Z. japonica* in Washington State, enabling the State to address questions regarding the genetic diversity and biology of *Z. japonica* in its native vs. introduced range. Additionally, genetic analysis could support the non-native status of *Z. japonica* in the Pacific Northwest and could show whether it arrived in a single or through multiple introductions. This information has the potential to guide management regarding future distribution patterns.

Little genetic research has been done on *Z. japonica* at this time. In 2006 a study was executed in Japan to address patch size and corresponding genetic diversity (Araki and Kunii 2006). These authors found that the larger the patch the more genetic diversity per patch; however, only one allozyme locus was analyzed and the study took place at only one site. The only other genetic

work on *Z. japonica* was the building of a molecular phylogenetic tree of the *Zosteraceae*, the family under which *Z. japonica* is placed (Tanaka et al. 2003).

Research using phylogenetic techniques has been done on *Z. marina* and these studies could be useful for guiding future questions on *Z. japonica*. For example, more genetically diverse populations of *Z. marina* increase in area faster than less diverse populations (Reusch et al. 2005). If the same is true for *Z. japonica*, genetic analysis and linked ecological experiments would contribute to our currently limited understanding of the invasive spread of *Z. japonica* in Washington and south along the Pacific coastline. The same study (Reusch et al. 2005) found that invertebrate abundance increased in more genetically diverse *Z. marina* beds. Another study, by Ruckelshaus (1996), showed *Z. marina* to have very small genetic neighborhoods, so that within one large bed (False Bay, WA) breeding only occurred between small patches. Additionally, Wyllie-Echeverria et al. (2010) found a high degree of genetic structure and clonal diversity in *Z. marina* populations in the San Juan Archipelago. Without doing the genetic processing of *Z. japonica* it will be impossible to understand how its genetic diversity is affecting its species interactions, abundance and expanding distribution.

Research discussion points from status and genetic variation session:

Suggestions for research:

1. What is the genetic divergence in the east and west Pacific, and does this confirm introduced status?
2. Population genetics should be used to compare patterns in genetic structure of *Z. japonica* to *Z. marina* in the Pacific Northwest.
3. Is there an underlying genetic basis for the physiological differences observed between populations?
4. Determine if genetic variation in *Z. japonica* is neutral or adaptive?
5. Does genetic diversity in *Z. japonica* influence ecosystem function?
6. Can genetic signals of climax vs. pioneering populations be seen in different *Z. japonica* sites?
7. Does *Z. japonica* hybridize with *Z. marina*?

Research Priorities

The group identified the following research priorities, which are *not* listed in order of importance.

- Continue compiling existing *Z. japonica* literature (primary, grey, unpublished) to identify future research priorities and find gaps in current knowledge.
 - Mine local knowledge, and connect scientists, managers, and the aquaculture industry to address future research goals.
- Encourage citizen monitoring, and train citizens in *Z. japonica* vs. *Z. marina* identification. Include information about *Z. marina*'s multiple morphotypes and phenotypic plasticity.
 - Produce a *Z. japonica* atlas for tracking the distribution of *Z. japonica* in Washington
- Expand our knowledge of *Z. japonica*'s effect on community dynamics and ecosystem function, and how these interactions impact ecosystem services produced in Washington State.
 - How does *Z. japonica* interact with other macrophytes, especially *Z. marina*? Do they compete?
 - In Willapa Bay and other sites, what are the ecological and economic impacts of mudflat vs. *Z. japonica* vs. aquaculture species vs. both together as a mosaic?
 - How is *Z. japonica* utilized by commercial and recreational fisheries (especially juvenile salmon), protected species, waterfowl, migratory shorebirds, and wading birds? How does *Z. japonica* affect the population dynamics of these species?
 - What is the economic value of net gain/loss of *Z. japonica*, or of efforts to manage this plant? What is the ecological and economic value of *Z. japonica* ecosystem services?
 - How do endangered species use or avoid *Z. japonica* (Endangered Species Act listed species such as Chinook and Chum salmon, Green Sturgeon, Bocaccio, etc.)?
- Confirm *Z. japonica*'s non-native status in Washington State and use genetic tools to predict expansion and responses to climate shifts
 - Use genetic tools (microsatellite markers, molecular clocks) to link eastern and western Pacific *Z. japonica* populations, which will help to determine the native/non-native status of *Z. japonica* in Washington.

- Determine the degree of neutral and adaptive genetic variation in *Z. japonica*. This data can be used to predict expansion, predict physiological and reproductive responses of *Z. japonica* to climatic shifts or other environmental changes.

References:

- Abe, M., K. Yokota, A. Kurashima, and M. Maegawa. 2009a. High water temperature tolerance in photosynthetic activity of *Zostera japonica* Ascherson & Graebner seedlings from Ago Bay, Mie Prefecture, central Japan. *Fisheries Science* **75**:1117-1123.
- Abe, M., K. Yokota, A. Kurashima, and M. Maegawa. 2009b. Temperature characteristics in seed germination and growth of *Zostera japonica* Ascherson & Graebner from Ago Bay, Mie Prefecture, central Japan. *Fisheries Science* **75**:921-927.
- Almasi, K. and P. Eldridge. 2008. A dynamic model of an estuarine invasion by a non-native seagrass. *Estuaries and Coasts* **31**:163-176.
- Araki, S. and H. Kunii. 2006. Allozymic implications of the propagation of eelgrass *Zostera japonica* within a river system. *Limnology* **7**:15-21.
- Baldwin, J. R. and J. R. Lovvorn. 1994. Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. *Marine Ecology Progress Series* **103**:119-127.
- Bando, K. J. 2006. The roles of competition and disturbance in a marine invasion. *Biological Invasions* **8**:755-763.
- Berkenbusch, K., A. A. Rowden, and T. E. Myers. 2007. Interactions between seagrasses and burrowing ghost shrimps and their influence on infaunal assemblages. *Journal of Experimental Marine Biology and Ecology* **341**:70-84.
- Berry, H. D., A. T. Sewell, S. Wyllie-Echeverria, B. R. Reeves, T. F. Mumford Jr., J. Skalski, R. C. Zimmerman, and J. Archer. 2003. Puget Sound Submerged Vegetation Monitoring Project: 2000-2002 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, WA.
- Bigley, R. E. and J. L. Barreca. 1982. Evidence for synonymizing *Zostera americana* den Hartog with *Zostera japonica* Aschers and Graebn. *Aquatic Botany* **14**:349-356.
- Britton-Simmons, K. H., S. Wyllie-Echeverria, E. K. Day, K. P. Booth, K. Cartwright, S. Flores, C. C. Garcia, T. L. Higgins, C. Montanez, A. Rames, K. M. Welch, and V. Wyllie-Echeverria. 2010. Distribution and performance of the nonnative seagrass *Zostera japonica* across a tidal height gradient on Shaw Island, Washington. *Pacific Science* **64**:187-198.
- Bulthuis, D. A. 1995. Distribution of seagrasses in a North Puget Sound estuary: Padilla Bay, Washington, USA. *Aquatic Botany* **50**:99-105.

- Bulthuis, D. A. and P. Margerum. 2005. Nutrients in an eelgrass dominated bay: Seasonal and diurnal fluctuations in dissolved inorganic nitrogen and phosphorus. *in* Puget Sound Georgia Basin Research Conference, Seattle, WA.
- Carlton, J. T. 2009. Deep Invasion Ecology and the Assembly of Communities in Historical Time. Pages 13-56 *in* G. Rilov and J. A. Crooks, editors. *Biological Invasions in Marine Ecosystems*. Springer-Verlag, Berlin Heidelberg.
- Chew, K. K. 1984. Recent advances in the cultivation of mollusks in the Pacific, United States and Canada. *Aquaculture* **39**:69-81.
- Clinton, W. J. 1999. Executive Order 13112 of February 3, 1999. *Federal Register* **64**(Doc no. 25): 6183-6186.
- Colautti, R. I. and H. J. MacIsaac. 2004. A neutral terminology to define invasive species. *Diversity and Distributions* **10**:135-141.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* **97**:153-166.
- denHartog, C. 1970. *The Sea-grasses of the World*. North-Holland Publishing Company, Amsterdam, Netherlands.
- Dowty, P., B. R. Reeves, H. Berry, S. Wyllie-Echeverria, T. F. Mumford Jr., A. T. Sewell, P. Milos, and R. Wright. 2005. Puget Sound Submerged vegetation Monitoring Project: 2003-2004 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, Washington.
- Dumbauld, B. R. and S. Wyllie-Echeverria. 2003. The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. *Aquatic Botany* **77**:27-42.
- Echavarría-Heras, H. A., E. Solana-Arellano, and E. Franco-Vizcaíno. 2006. The role of increased sea surface temperature on eelgrass leaf dynamics: Onset of El Niño as a proxy for global climate change in San Quintín Bay, Baja California *Bulletin of the Southern California Academy of Science* **105**:113-127.
- Gaeckle, J., P. Dowty, H. Berry, and L. Ferrier. 2009. Puget Sound Submerged Vegetation Monitoring Project: 2008 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, WA.

- Gaeckle, J., P. Dowty, H. Berry, S. Wyllie-Echeverria, and T. F. Mumford Jr. 2008. Puget Sound Submerged Vegetation Monitoring Project: 2006-2007 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, WA.
- Gaeckle, J., P. Dowty, B. R. Reeves, H. Berry, S. Wyllie-Echeverria, and T. F. Mumford Jr. 2007. Puget Sound Submerged Vegetation Monitoring Project: 2005 Monitoring Report. Nearshore Habitat Program, Washington State Department of Natural Resources, Olympia, Washington.
- Hahn, D. R. 2003. Alteration of microbial community composition and changes in decomposition associated with an invasive intertidal macrophyte. *Biological Invasions* **5**:45-51.
- Harrison, P. G. 1976. *Zostera japonica* Aschers. & Graebn. in British Columbia, Canada. *Syesis* **9**:359-360.
- Harrison, P. G. 1982. Comparative growth of *Zostera japonica* Aschers. & Graebn. and *Z. marina* L. under simulated intertidal and subtidal conditions. *Aquatic Botany* **14**:373-379.
- Harrison, P. G. 1987. Natural expansion and experimental manipulation of seagrass *Zostera* spp abundance and the response of infaunal invertebrates. *Estuarine Coastal and Shelf Science* **24**:799-812.
- Harrison, P. G. and R. E. Bigley. 1982. The recent introduction of the seagrass *Zostera japonica* Aschers. & Graebn. to the Pacific coast of North America. *Canadian Journal of Fisheries and Aquatic Sciences* **39**:1642-1648.
- Hemminga, M. A. and C. M. Duarte. 2000. *Seagrass Ecology*. Cambridge University Press, Cambridge, UK.
- Hershner, C. and K. Havens. 2008. Managing invasive aquatic plants in a changing system: Strategic consideration of ecosystem services. *Conservation Biology* **22**:544-550.
- Hitchcock, C. L., A. Cronquist, M. Ownbey, and J. W. Thompson. 1969. *Vascular plants of the Pacific Northwest, Part 1: Vascular cryptogams, gymnosperms, and monocotyledons*. Univ. Washington Press, Seattle, WA.
- Johnson, M. R., S. L. Williams, C. H. Lieberman, and A. Solbak. 2003. Changes in the abundance of the seagrasses *Zostera marina* L. (eelgrass) and *Ruppia maritima* L. (widgeongrass) in San Diego, California, following an El Niño event. *Estuaries* **26**:106-115.

- Kaldy, J. E. 2006. Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Ascher. & Graeb.), in a Pacific Northwest estuary, USA. *Hydrobiologia* **533**:201-217.
- Kaldy, J. E. and D. J. Shafer. *Submitted*. *Zostera japonica* mortality in response to extreme high temperature. *Aquatic Botany*.
- Larned, S. T. 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary. *Marine Ecology Progress Series* **254**:69-80.
- Lovvorn, J. R. and J. R. Baldwin. 1996. Intertidal and farmland habitats of ducks in the Puget Sound region: A landscape perspective. *Biological Conservation* **77**:97-114.
- McKinnon, J. G., P. E. Gribben, A. R. Davis, D. F. Jolley, and J. T. Wright. 2009. Differences in soft-sediment macrobenthic assemblages invaded by *Caulerpa taxifolia* compared to uninvaded habitats. *Marine Ecology Progress Series* **380**:59-71.
- Miller, G. H. 1977. Eelgrass distribution, density, leaf length and standing stock in Grays Harbor, 1977. Seattle District, Army Corps of Engineers, Seattle, WA. Report # DACW67-77-M-1240.
- Neira, C., L. A. Levin, and E. D. Grosholz. 2005. Benthic macrofaunal communities of three sites in San Francisco Bay invaded by hybrid *Spartina*, with comparison to uninvaded habitats. *Marine Ecology Progress Series* **292**:111-126.
- Nelson, T. A. 1997. Interannual variance in a subtidal eelgrass community. *Aquatic Botany* **56**:245-252.
- Nomme, K. M. and P. G. Harrison. 1991a. A multivariate comparison of the seagrasses *Zostera marina* and *Zostera japonica* in monospecific versus mixed populations. *Canadian Journal of Botany* **69**:1984-1990.
- Nomme, K. M. and P. G. Harrison. 1991b. Evidence for interaction between the seagrasses *Zostera marina* and *Zostera japonica* on the Pacific coast Canada. *Canadian Journal of Botany* **69**:2004-2010.
- Norris, J. G., S. Wyllie-Echeverria, T. Mumford, A. Bailey, and T. Turner. 1997. Estimating basal area coverage of subtidal seagrass beds using underwater videography. *Aquatic Botany* **58**:269-287.
- Occhipinti-Ambrogi, A. and B. S. Galil. 2004. A uniform terminology on bioinvasions: A chimera or an operative tool? *Marine Pollution Bulletin* **49**:688-694.

- Phillips, R. 1984. The ecology of eelgrass meadows in the Pacific Northwest: A community profile. US Fish & Wildlife Service Report OBS-84/24.
- Phillips, R. C. and R. F. Shaw. 1976. *Zostera noltii* Hornem. in Washington, USA. *Syesis* **9**:355-358.
- Posey, M. H. 1988. Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. *Ecology* **69**:974-983.
- Reusch, T. B. H., A. Ehlers, A. Hammerli, and B. Worm. 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences USA* **102**:2826-2831.
- Ruckelshaus, M. H. 1996. Estimation of genetic neighborhood parameters from pollen and seed dispersal in the marine angiosperm *Zostera marina* L. *Evolution* **50**:856-864.
- Ruesink, J., B. Feist, C. Harvey, J. Hong, A. Trimble, and L. Wisheart. 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. *Marine Ecology Progress Series* **311**:203-215.
- Ruesink, J. L., J. S. Hong, L. Wisheart, S. D. Hacker, B. R. Dumbauld, M. Hession-Lewis, and A. C. Trimble. 2010. Congener comparison of native (*Zostera marina*) and introduced (*Z. japonica*) eelgrass at multiple scales within a Pacific Northwest estuary. *Biological Invasions* **12**:1773-1789.
- Sakai, A. K., F. W. Allendorf, J. S. Holt, D. M. Lodge, J. Molofsky, K. A. With, S. Baughman, R. J. Cabin, J. E. Cohen, N. C. Ellstrand, D. E. McCauley, P. O'Neil, I. M. Parker, J. N. Thompson, and S. g. Weller. 2001. The population biology of invasive species. *Ecology, Evolution, and Systematics* **32**:305-332.
- Semmens, B. X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:2053-2062.
- Shafer, D. J. 2007. Physiological factors affecting the distribution of the non-indigenous seagrass *Zostera japonica* along the Pacific coast of North America. Ph.D Dissertation. University of South Alabama, Mobile, AL.
- Shafer, D. J., J. E. Kaldy, T. D. Sherman, and K. M. Marko. *In review*. Effects of salinity on photosynthesis and respiration of the seagrass *Zostera japonica*: A comparison of two established populations in North America. Submitted to *Aquatic Botany*.

- Shafer, D. J., T. D. Sherman, and S. Wyllie-Echeverria. 2007. Do desiccation tolerances control the vertical distribution of intertidal seagrasses? *Aquatic Botany* **87**:161-166.
- Shafer, D. J., S. Wyllie-Echeverria, and T. D. Sherman. 2008. The potential role of climate in the distribution and zonation of the introduced seagrass *Zostera japonica* in North America. *Aquatic Botany* **89**:297-302.
- Short, F. T. and R. G. Coles. 2001. *Global Seagrass Research Methods*. Elsevier Science B.V., Amsterdam.
- Short, F. T. and H. A. Neckles. 1999. The effects of global climate change on seagrasses. *Aquatic Botany* **63**:169-196.
- Shull, S. and D. Bulthuis. 2002. A methodology for mapping current and historical coverage of estuarine vegetation with aerial photography and ArcView. Washington State Department of Ecology, Padilla Bay National Estuarine Research Reserve, Mount Vernon, Washington. Tech Report No. 26.
- Simenstad, C. 1994. Faunal associations and ecological interactions in seagrass communities of the Pacific Northwest coast. Pages 11-18 *in* S. Wyllie-Echeverria, A. M. Olson, and M. J. Hershman, editors. *Seagrass science and policy in the Pacific Northwest: Proceedings of a seminar series (SMA 94-1)*, EPA 910/R-94-004.
- Simenstad, C., J. Cordell, R. Wissmar, K. Fresh, S. Schroder, M. Carr, G. Sanborn, and M. Burg. 1988. Assemblage structure, microhabitat distribution and food web linkages of epibenthic crustaceans in Padilla Bay National Estuarine Research Reserve, Washington. NOAA Technical Report, Marine & Estuarine Management Division, NOAA grant no. NA86AA-D-CZ028.
- Snover, A. K., P. W. Mote, L. Whitely Binder, A. F. Hamlet, and N. J. Mantua. 2005. *Uncertain future: Climate change and its effects on Puget Sound*. A report for the Puget Sound Action Team by the Climate Impacts Group. Center for Science in the Earth System, Joint Institute for the Study of the Atmosphere and Oceans, University of Washington, Seattle.
- Tanaka, N., J. Kuo, O. Y, M. Nakaoka, and K. Aioi. 2003. Phylogenetic relationships in the genera *Zostera* and *Heterozostera* (Zosteraceae based on matK sequence data). *Journal of Plant Research* **116**:273-279.
- Thom, R. 1984. Composition, habitats, seasonal changes and productivity of macroalgae in Grays Harbor Estuary, Washington *Estuaries* **7**:51-60.

- Thom, R., B. Miller, and M. Kennedy. 1995. Temporal patterns of grazers and vegetation in a temperate seagrass system. *Aquatic Botany* **50**:201-205.
- Thomsen, M. S., T. Wernberg, B. R. Silliman, and F. Tuya. 2009. Evidence for impacts of non-indigenous macroalgae: A meta-analysis of experimental field studies. *Journal of Phycology* **45**:812-819.
- Tomlinson, P. B. and U. Posluzny. 2001. Generic limits in the seagrass family Zosteraceae. *Taxon* **50**:429-437.
- Tsai, C., S. Yang, A. C. Trimble, and J. L. Ruesink. 2010. Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. *Marine Biology* **157**:1929-1936.
- Wyllie-Echeverria, S., S. L. Talbot, and J. R. Rearick. 2010. Genetic structure and diversity of *Zostera marina* (eelgrass) in the San Juan archipelago, Washington, USA. *Estuaries and Coasts* **33**:811-827.
- Zavaleta, E. 2000. The economic value of controlling an invasive shrub. *AMBIO* **29**:462-467.