Carbon draw-down potential by the native eelgrass *Zostera marina* in Puget Sound and implications for ocean acidification management

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Abstract

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In 2012, the Washington State Blue Ribbon Panel on Ocean Acidification recommended actions to address local impacts of ocean acidification. At least two of these actions included a focus on seagrasses. Recognizing the ability of the native seagrasses *Z. marina* to remove carbon from seawater, the panel identified the need to “preserve Washington’s existing native seagrass and kelp populations and, where possible, restore these populations” and to “develop vegetation-based systems of remediation for use in upland habitats and in shellfish areas”. In this research I take the first steps to evaluate the potential utility of the native eelgrass *Z. marina* as a tool for mitigation of ocean acidification in Puget Sound. Using estimates of eelgrass abundance and distribution and regional estimates of net primary productivity, I estimated at relatively coarse scales the annual amount of carbon that could be removed from seawater by eelgrass via photosynthetic assimilation of carbon. I did not estimate long-term sequestration or burial. I applied a simple model to estimate the potential for carbon removal from seawater at several locations where eelgrass is present. At the basin level, rates of carbon removal by *Z. marina* are on the order of 10^{10} gC y^{-1} for the Puget Sound Basin, and range from 10^{8} to 10^{10} gC y^{-1} for individual sub-basins. Initial estimates suggest that at most of the selected sites, the change in dissolved inorganic carbon (DIC) resulting from seagrass carbon assimilation may not be sufficient to cause a pronounced shift in carbonate chemistry. This first estimate of carbon draw-down potential suggests that *Z. marina* has limited ability to serve as a tool to ameliorate effects of ocean acidification in Puget Sound.

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INTRODUCTION

The ocean plays significant economic, social, and ecological roles in our society. It is estimated that the annual value of services from the world's oceans exceeds $25 trillion USD per year (Martínez et al. 2007). The ocean also plays a critical role in the global carbon cycle. Approximately 93% (40 Tt) of the Earth's CO_2 is stored and cycled through the ocean; the ocean therefore represents one of the largest long-term sinks for carbon on the planet (Nelleman et al. 2009). Since the beginning of the industrial era, the ocean has absorbed approximately one-third of the total anthropogenic CO_2 (Sabine et al. 2004). The continual uptake of CO_2 by the ocean changes the biogeochemical carbonate balance and reduces seawater pH, leading to ocean acidification (Gattuso and Buddemeier 2000, Pörtner et al. 2004). Increasing CO_2 levels in combination with a loss of the ocean's ability to act as an efficient carbon sink is of great concern (Doney et al. 2009). The consequent threats to marine life are especially difficult to predict.

The carbon captured though biological processes in the ocean is referred to as blue carbon. Blue carbon sinks include some of the most productive habitats in the world. Productive habitats are mainly net autotrophic, meaning that the CO_2 fixed by photosynthesis exceeds that respired back to the atmosphere, thereby removing CO_2 from both the atmosphere and ocean (Duarte and Cebrian 1996, Gattuso et al. 1998, Duarte et al. 2005, Kaladharan et al. 2009). Captured by living organisms in the ocean, some of the strongest carbon sinks on the planet are marine vegetated habitats such as mangrove swamps, salt marshes, and seagrass beds where the carbon burial capacity is about 180 times greater than in the open ocean. Despite covering less than 0.5% of the sea bed, these vegetated habitats account for 50-71% of all carbon storage in the ocean (Nelleman et al. 2009). In the ocean, carbon is stored in the sediments; and unlike terrestrial rainforests where carbon is stored on the order of thousands of years, carbon in these marine sediment layers can stay buried for millennia (Mateo et al. 1997, Nelleman et al. 2009). However, many of these vegetated habitats are experiencing sharp global declines (Nelleman et al. 2009, Duarte et al. 2011). The rate of loss of these habitats is higher than for any other habitat on the planet: in some cases the rate of loss is up to four times that of rainforests like the Amazon, which has been assumed to be the largest terrestrial carbon sink (Nelleman et al. 2009, Duarte et al. 2010). The maintenance of marine vegetation habitats as blue carbon sinks is thought to be important for local adaptation strategies to reduce the susceptibility of human coastal communities to the consequences of ocean acidification (Nelleman et al. 2009).

Of the three vegetated habitats (mangrove, saltmarsh, and seagrass) that have the potential to be strong carbon sinks, seagrasses are the most widely distributed globally. Although seagrass meadows account for only a tiny fraction of the coastal ocean (0.1%), they provide critical ecosystem goods and services where they occur (Costanza et al. 1997). Seagrass meadows are often considered critical nursery, forage, and migration habitat for ecologically and economically important nearshore species (Gaeckle 2011). However, like mangroves and salt marshes, seagrass habitats are rapidly declining. A recent global assessment of seagrass extent by (Waycott et al. 2009) indicates that about one-third of all seagrass area has already been lost. With this decline comes a corresponding loss in a local and efficient source of carbon draw-down. According to Duarte et al. (2005), the annual rate of carbon accumulation in seagrass meadows is almost two times larger than that of most terrestrial ecosystems. Seagrasses are estimated to bury a minimum of 27.4 $TgCyr^{-1}$, which is approximately 10% of the annual organic C burial in the world's ocean (Duarte et al. 2005, Fourqurean et al. 2012).

Because of their high productivity rates, seagrasses are able to store large amounts carbon by taking up carbon from the surrounding water and burying it deep in sediment layers (Thom et al. 2003, Duarte et al. 2011) (Figure 1). According to Koch et al. (2013), as a C3 type plant, seagrasses are also likely to be competitively dominant under acidified conditions because of their ability to take in additional dissolved inorganic carbon DIC even under elevated CO_2 conditions. Unlike photosynthesis in C4 plants, photosynthesis in C3 plants continues to increase with increasing CO_2 (to some maximum), thereby increasing the amount of carbon assimilated by the plant (Koch et al. 2013). In addition to its capacity to assimilate and store carbon in sediments, carbon stored in seagrass leaves can be exported from the system as currents carry away detritus to deeper areas where additional burial can occur (Thom et al. 2003, Kennedy et al. 2010) (Figure 1). Consequently, seagrass beds that occur in proximity to submarine canyons and other deep areas have added potential to contribute to the sequestration of ocean carbon.

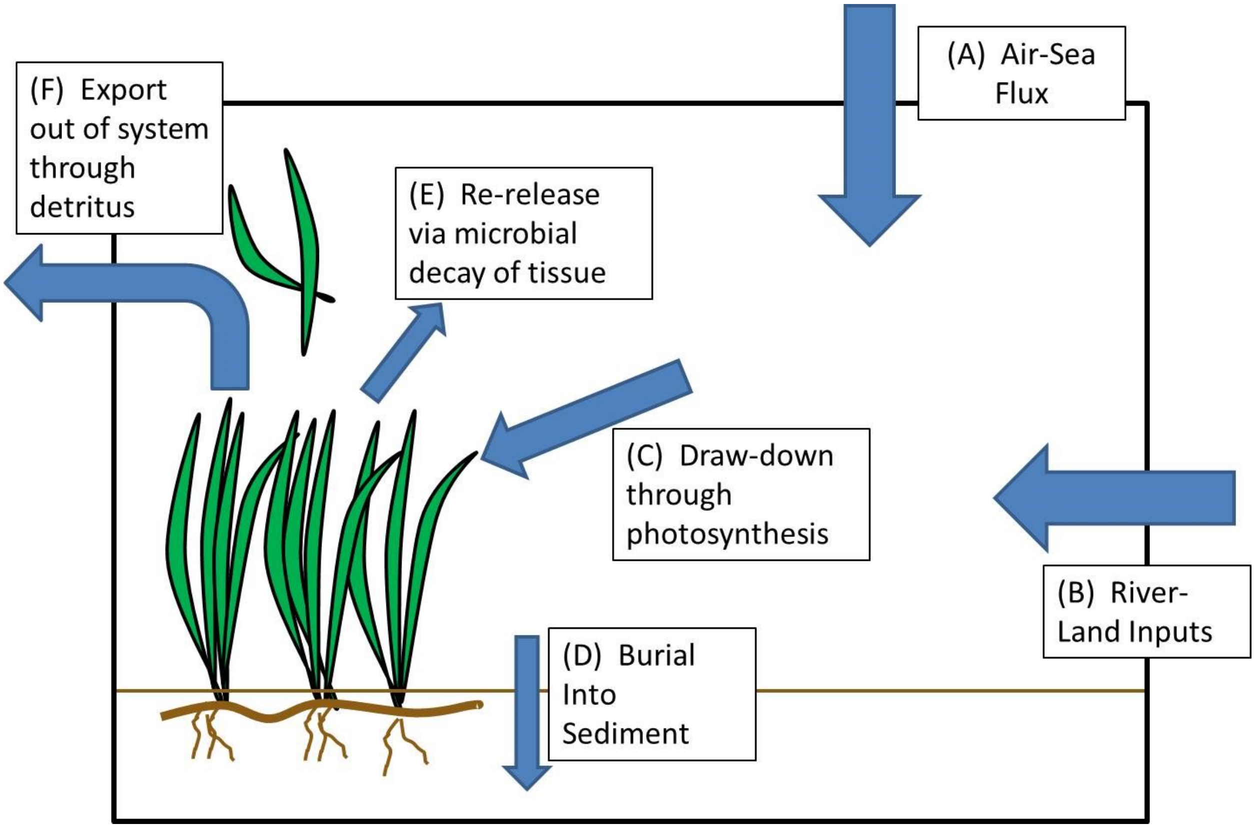

Figure 1. Conceptual diagram of carbon flow in an eelgrass bed. A) Carbon is added into the system through atmospheric CO_2 absorbed into the ocean, B) runoff from the river and land introduces additional carbon, C) *Z. marina* assimilates carbon from the water column through metabolic processes, D) a proportion of carbon that is assimilated by *Z. marina* is buried in the sediments, E) some carbon is re-released into the water column via microbial decay of seagrass tissue and plant respiration, and F) a proportion of carbon is exported out of the system through detritus carried away through currents or tides.

The seagrass *Zostera marina* is native to the west coast of the U.S. and is the most abundant seagrass species in Washington State (Berry et al. 2003). It is one of approximately 50 species of seagrass worldwide and is widely distributed throughout the northern hemisphere (Thom et al. 2003). While six species of seagrass occur in the Pacific Northwest, *Z. marina* is by far the dominant seagrass in terms of biomass and areal extent, extending from southeastern Alaska to Baja California, Mexico (Wyllie-Echeverria and Ackerman 2003, Kaldy 2006). Because of its prevalence throughout the inland waters of Puget Sound in Washington State, *Z. marina* has the potential to serve as a local sink of carbon and thereby could provide a valuable tool for mitigation of local effects of ocean acidification.

In 2012, the Washington State Blue Ribbon Panel on Ocean Acidification recommended actions to address local impacts of ocean acidification. At least two of these actions included a focus on seagrasses. Recognizing the ability of the native seagrasses *Z. marina* to draw-down and store excess carbon over long periods of time, the panel identified the need to "preserve Washington's existing native seagrass and kelp populations and, where possible, restore these populations" (Action 6.3.1) and to "develop vegetation-based systems of remediation for use in upland habitats and in shellfish areas" (Action 6.1.1) (Adelsman and Whitely-Binder 2012).

In Puget Sound, both seagrasses and kelps have potential utility in carbon draw-down in shallow nearshore areas. Here, I restrict my inquiry to seagrasses and take the first steps to evaluate the potential utility of *Z. marina* as a source of carbon draw-down in Puget Sound. I define the term *carbon draw-down* as the metabolic assimilation rate of carbon by the seagrass *Z. marina*. I restricted my analysis to carbon assimilation and did not estimate carbon sequestration or burial. I first estimated the abundance and distribution of *Z. marina* in Puget Sound and then estimated the draw-down capacity of *Z. marina* for the entire Puget Sound and within each sub-basin of Puget Sound. I further applied a more detailed draw-down model modified from Unsworth et al. (2012) to several individual locations around the Puget Sound basin.

METHODS

Study Area

I used data obtained from the Washington Department of Natural Resources (DNR) to estimate the distribution and abundance of seagrass in Puget Sound (DNR 2011). For consistency with the original data set, I defined Puget Sound as Washington State waters east of Cape Flattery at the entrance to the Strait of Juan de Fuca. Following the classification of DNR, I sub-divided Puget Sound into five sub-basins: Central Puget Sound, Hood Canal, North Puget Sound, San Juans-Strait of Juan de Fuca, and the Saratoga-Whidbey Basin (Figure 2). The most southern reaches of the Puget Sound basin were excluded from the DNR data set and therefore from my analysis because eelgrass rarely occurs in these areas (Berry et al. 2003). Each of these sub-basins differs substantially in physical features including bathymetry, circulation, river inputs, nutrient inputs, urban development, and carbonate chemistry (Gustafson et al. 2000). They also differ in some ecological features, including the abundance and distribution of seagrass.

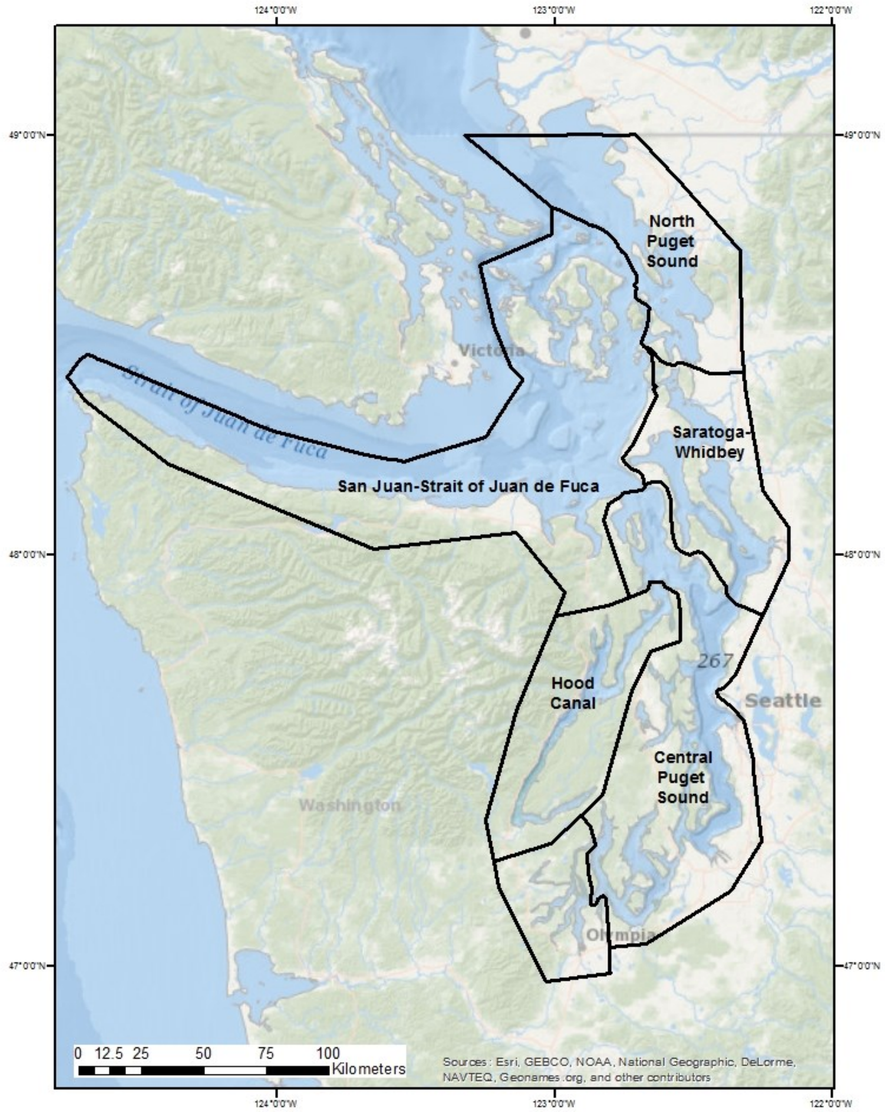

Figure 2. Basins of Puget Sound as defined by the DNR in SVMP Report: North Puget Sound, Saratoga-Whidbey Basin, San Juan Straits, Hood Canal, Central Puget Sound. The most southern reaches of the Puget Sound Basin were excluded from analysis. Reproduced with permission from DNR.

Abundance and Distribution Analysis

I used the Submerged Vegetation Monitoring Project (SVMP) GIS data set produced by the DNR. The SVMP project surveys the status and trends of *Z. marina* in Puget Sound and includes annual surveys of abundance and distribution from 2000 to 2011 (Gaeckle 2011). The SVMP data include measurements of the area occupied by *Z. marina* estimated from the ordinary high water (OHW) to -20 feet mean lower low water (MLLW). Most estimates were made during the months between June and October, which is the optimal growing period for nearshore marine vegetation (Berry et al. 2003).

Using ArcGIS 10.1, I calculated the total maximum and minimum extent of *Z. marina* beds in Puget Sound based on the data reported by DNR. Because this was a multi-year study and the sampling regime, as defined by DNR, only allowed for a two- to three-year sampling rotation for most eelgrass beds, I defined maximum extent for each eelgrass bed as the greatest extent measured over the project period. Similarly, I defined minimum extent as the smallest areal extent measured over the project period. Because *Z. marina* beds are known to fluctuate in areal extent between years (Gaeckle 2011), this method allowed me to calculate upper and lower bounds of carbon draw-down potential, bound by the largest and smallest extent of *Z. marina* measured in Puget Sound over the past decade.

Carbon Draw-down Potential

Only a handful of published estimates of carbon draw-down exist and most work has been performed in the tropics or on seagrass species other than *Z. marina*. Therefore, I used net primary production (NPP) as an estimate of carbon draw-down by seagrass. Net primary production can be used as a proxy for carbon draw-down from seawater because it is a measure of the amount of carbon the eelgrass assimilates from the surrounding environment (e.g. Gattuso et al. (1998), Duarte et al. (2010)). This technique has been used by others (Smith 1981, Duarte et al. 2005, Kennedy et al. 2010).

Because carbon assimilation is likely to vary based on local environmental conditions, I searched the available literature for estimates of NPP of *Z. marina* in the Puget Sound region. To establish upper and lower bounds of carbon draw-down potential of Puget Sound, I used the largest and smallest values of NPP reported in the literature for the Puget Sound region.

I applied the NPP rates from the upper and lower estimates and multiplied those rates by estimates of the area occupied by *Z. marina* to calculate the carbon draw-down potential of the entire Puget Sound Basin. I repeated this calculation for each sub-basin.

An example calculation :

$$NPP\ (gC\ m^{-2}y^{-1})\ \times\ aerial\ extent\ of\ Z.marina\ bed\ (m^{2})$$

$$= total\ carbon\ drawdown\ per\ year\ for\ Puget\ Sound\ (gCy^{-1})$$

Because the DNR GIS data set does not include density estimates, I assumed equal densities across all sampling locations at the level of basin and sub-basin. This simplistic but necessary assumption can be refined as new data become available.

Selected Locations

I selected four locations within the Puget Sound Basin to investigate in greater detail. These sites were chosen based on three criteria to include areas where 1) *Z. marina* is actively monitored, 2) the threat of ocean acidification is of concern to managers or shellfish growers, or 3) environmental variables were available from the published literature or DNR GIS data set.

Based on the three criteria, I selected four selected sites: Padilla Bay, Picnic Cove, Jamestown, and Quilcene/Dabob Bay (Figure 3).

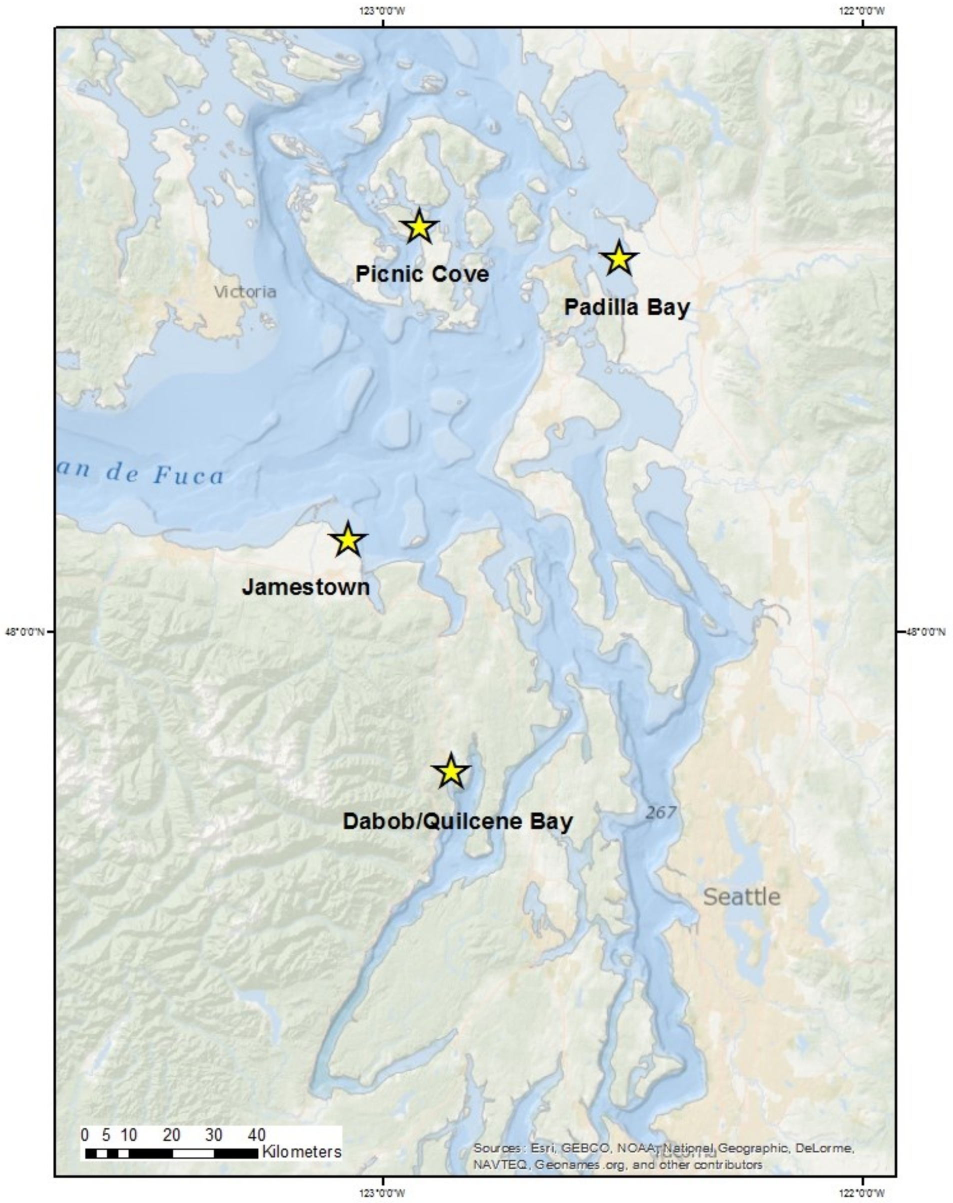

Figure 3. Map of selected site locations in Puget Sound, WA. Selected sites include (from north to south) Picnic Cove, Padilla Bay, Jamestown, and Dabob/Quilcene Bay.

Following the model developed by Unsworth et al. (2012) (Table 1), I calculated the predicted change in dissolved inorganic carbon (DIC) concentration in seagrass beds that could be attributed to carbon assimilation by seagrass. I used reported values of background DIC (i.e., DIC measurements taken from the sub-basin but not from the specific location of the seagrass bed) from recent work performed in Puget Sound (Feely et al. 2010, Sullivan 2012, Love *unpublished data*).

For the purposes of the model, the estimated volume of receiving water was calculated as a 1m^2 sample plot multiplied by the average depth of the eelgrass bed at each site as calculated from SVMP transect data. The daily dilution rate was estimated based on a semi-diurnal tidal cycle. The daily dilution rate assumed that for six hours per day, the entire eelgrass bed was submerged. During the six-hour period, my model assumed the eelgrass was drawing carbon from surrounding water through metabolic processes, as estimated by NPP. I used the carbonate chemistry calculator CO2sys (Lewis et al. 1998) to estimate the change in pH that could be produced by the modeled changes in seawater DIC. The CO2sys program requires the input of other variables including total alkalinity (TA), salinity, temperature, pressure, and nutrient data (phosphorus and silica). Total alkalinity values for each site were taken from the most local estimates available from the published literature; Padilla Bay, Jamestown and Dabob Bay values were taken from Feely et al. (2010) and Picnic Cove TA values were taken from Sullivan (2012). Temperature, pressure, and salinity values were taken from Sullivan (2012).

Table 1. Model used to predict change in seawater DIC over *Z. marina* bed due to metabolic assimilation of carbon. Modified from Unsworth et al. (2012).

Equation
$C = B - [\frac{P}{V} d]$

Parameters	Description
C	Final seagrass meadow seawater DIC (μmolCl^{-1})
B	Background seawater DIC (μmolCl^{-1})
P	*Z. marina* net primary productivity (μmolCm^{-2}day^{-1})
V	Volume of receiving water (liters)
d	Daily dilution rate/residence time of receiving water (hours day^{-1})

RESULTS

The estimated areal extent of *Z. marina* in Puget Sound ranged from 9.69×10^7 m^2 to 1.17×10^8 m^2 (Table 2). Among sub-basins, estimated abundance was greatest in North Puget Sound and smallest in Central Puget Sound.

Table 2. Extent of *Z. marina* bed area in Puget Sound by sub-basin.

	Areal Extent (minimum estimate) (m^2)	Areal Extent (maximum estimate) (m^2)
Central Puget Sound	2.86×10^6	3.47×10^6
Hood Canal	5.36×10^6	7.89×10^6
North Puget Sound	5.90×10^7	7.04×10^7
San Juans- Strait of Juan de Fuca	1.25×10^7	1.55×10^7
Saratoga-Whidbey Basin	1.72×10^7	2.01×10^7
TOTAL Puget Sound Basin	9.69×10^7	1.17×10^8

I multiplied high and low values of NPP reported in the literature (199.7 to 341.82 gC m^{-2} y^{-1}; Thom 1990; 2008) by high and low estimates of seagrass extent to estimate carbon draw-down rates in the Puget Sound basins and each of the four sub-basins (Table 3). Results suggest carbon assimilation rates are on the order of 10^{10} gC y^{-1} for Puget Sound Basin, and range from 10^{8} to 10^{10} gC y^{-1} for the sub-basins.

Table 3. Minimum and maximum estimates of the metabolic carbon sink capacity of *Z. marina*, in gC m^{-2} y^{-1}, using upper and lower bounds of NPP and minimum and maximum estimates of area occupied by *Z. marina.* Estimates are given for the entire Puget Sound and for individual sub-basins. Minimum estimates of NPP are based on Thom (1990); maximum estimates of NPP are based on Thom et al. (2008).

	Source	NPP (gC m^{-2} y^{-1})	Areal Extent (minimum estimate) (m^2)	C Draw-down Rate (minimum estimate) gC y^{-1}	Areal Extent (maximum estimate) (m^2)	C Draw-down Rate (maximum estimate) gC y^{-1}
Entire Basin	Minimum NPP	199.7	9.69×10^7	1.49×10^{10}	1.17×10^8	2.34×10^{10}
	Maximum NPP	255.5	9.69×10^7	3.31×10^{10}	1.17×10^8	4.01×10^{10}
Central Puget Sound	Minimum NPP	199.7	2.86×10^6	5.71×10^8	3.47×10^6	6.93×10^8
	Maximum NPP	255.5	2.86×10^6	9.77×10^8	3.47×10^6	1.19×10^9
Hood Canal	Minimum NPP	199.7	5.36×10^6	1.07×10^9	7.89×10^6	1.58×10^9
	Maximum NPP	255.5	5.36×10^6	1.83×10^9	7.89×10^6	2.70×10^9
North Puget Sound	Minimum NPP	199.7	5.90×10^7	1.18×10^{10}	7.04×10^7	1.41×10^{10}
	Maximum NPP	255.5	5.90×10^7	2.02×10^{10}	7.04×10^7	2.41×10^{10}
San Juan-Strait of Juan de Fuca	Minimum NPP	199.7	1.25×10^7	2.49×10^9	1.55×10^7	3.09×10^9
	Maximum NPP	255.5	1.25×10^7	4.36×10^9	1.55×10^7	5.29×10^9
Saratoga-Whidbey	Minimum NPP	199.7	1.72×10^7	3.44×10^9	2.01×10^7	4.02×10^9
	Maximum NPP	255.5	1.72×10^7	5.90×10^9	2.01×10^7	6.88×10^9

Padilla Bay

Padilla Bay is located in the North Puget Sound sub-basin and is one of six 'core' sites monitored annually by DNR (Gaeckle 2011). The site is part of the National Estuarine Research Reserve System. Z*ostera marina* occupies about 7.80 x 10^7 m^2 in Padilla Bay, making it one of the largest stands of seagrass in the Pacific Northwest. Seagrass in Padilla Bay grows at depths ranging from -7.16 to 1.77 meters relative to mean lower low water (MLLW). According to the DNR's most recent seagrass trend analysis, there has been no detectable trend in abundance of *Z. marina* in Padilla Bay from 2004-2009.

Picnic Cove, Shaw Island

Picnic Cove, on the east side of Shaw Island, lies within the San Juans-Strait of Juan de Fuca sub-basin. This site is occupied by about 7.14 x 10^4 m^2 of *Z. marina*. The depth at which eelgrass grows at this site ranges from -7.92 to 0.60 meters relative to MLLW. Like Padilla Bay and Jamestown, Picnic Cove is a 'core' site sampled annually by DNR. According to Gaeckle (2011), the eelgrass in Picnic Cove showed steady decline from 2004-2009.

Jamestown

Jamestown is located in the San Juans-Strait of Juan de Fuca sub-basin and is one of the six 'core' sites that has been sampled annually over the past ten years by DNR. Jamestown is occupied by about 1.13 x 10^7 m^2 of *Z. marina* growing at depths of -8.11 to 0.93 meters relative to MLLW. Contrary to the three other sites included here, the eelgrass in Jamestown showed an increasing trend in the extent of the eelgrass bed from 2004-2009 (Gaeckle 2011).

Quilcene/Dabob Bay

Dabob Bay is located in the Hood Canal sub-basin and is the location of a shellfish hatchery that has shown vulnerability to ocean acidification (Dickson 2010). Several *Z. marina* beds exist within the bay. The eelgrass bed closest to that hatchery (Flat 42 in the DNR data seat) includes ~2.43×10^6 m^2 of *Z. marina* growing in depths from -7.46 to 0.47 meters relative to MLLW. Although there is no detectable temporal trend in the areal extent of eelgrass in Flat 42, there is evidence of decline from 2004-2009 in nearby eelgrass beds and strong evidence of decline in *Z. marina* extent in the Hood Canal sub-basin (Gaeckle 2011).

Table 4. Change in DIC and pH for selected sites. DIC calculations are based on a model modified from Unsworth et al. (2012) and changes in pH were calculated in CO2sys. Low NPP values are based on Thom (1990); high NPP values are based on Thom et al. (2008).

Selected Site	NPP	+ %Δ in DIC for selected site	+ Δ in pH
Dabob Bay	Low	0.72	0.03
	High	1.23	0.05
Padilla Bay	Low	1.12	0.03
	High	1.91	0.05
Picnic Cove	Low	0.23	0.02
	High	0.40	0.03
Jamestown	Low	0.20	0.01
	High	0.34	0.02

The estimated percent change in DIC and pH due to carbon assimilation by *Z. marina* is greatest for Padilla Bay and smallest for Jamestown (Table 4). There is an unspecified amount of uncertainty associated with these estimates due to assumptions made in using CO2sys for these calculations. Even so, these changes in pH are comparable to those reported by Unsworth et al. (2012).

DISCUSSION

Here I provide a first theoretical estimate of the potential for draw-down of carbon from seawater by the seagrass *Zostera marina* in Puget Sound. Based on published measurements of net primary productivity, my results suggest that most *Zostera marina* beds in Puget Sound are net autotrophic and therefore have the ability to assimilate carbon from the local water column. However, my results suggest that the ability of *Z. marina* in Puget Sound to act as an effective tool to ameliorate the effects of ocean acidification is limited.

Results from my model suggested that carbon assimilation by *Z. marina*, based on published estimates of net primary production, was not enough to completely offset modern day increases in anthropogenic carbon. Feely et al. (2010) estimated that for surface waters in Puget Sound the anthropogenic DIC from the atmosphere increased 13-36 μmol kg^{-1} from the pre-industrial to the present. Even using the upper estimate of net primary productivity (341.82 gC m^{-2}yr^{-1}) from Thom et al. (2008), the maximum predicted change in DIC was only 31.74 μmol kg^{-1} at Padilla Bay, which is one of the largest stands of seagrass in the Pacific Northwest. A decline in DIC of 31.74 μmolkg^{-1} equates to an increase of only about 0.05 pH units (Table 4), which is insufficient to offset projected changes in pH due to ocean acidification reported in Feely et al. (2010). Work by Schulz et al. (2009) suggested that changes in DIC of less than 3% of the initial (or existing) concentration are unlikely to cause pronounced shifts in carbonate chemistry. The results of my model showed a maximum downward shift of 1.91% DIC at Padilla Bay due to carbon assimilation by *Z. marina*. To achieve approximately a 3% change in DIC at Padilla Bay, *Z. marina* would need to maintain a NPP rate of at least 535 gC m^{-2}yr^{-1}. If the findings of Schulz et al. (2009) can be extended to my analysis, then they suggest that carbon assimilation by *Z. marina* is not sufficient to cause a significant shift in local carbonate chemistry. However, work by Feely et al. (2009) found that Revelle factors (RF) (Revelle and Suess 1957) in Puget Sound are higher than the open-ocean RF values, suggesting that even small changes in DIC values can equate to significant changes in pH values.

Although the biological responses of organisms in Puget Sound to the effects of ocean acidification are not yet well quantified, a number of other studies suggest that calcifying organisms (e.g. urchins, oysters), are vulnerable to relatively small changes in pH, especially at early life history stages (Kurihara 2008, O'Donnell et al. 2009, Talmage and Gobler 2009, Hofmann et al. 2010). In recent years, a shellfish oyster hatchery located on Dabob Bay has experienced large mortalities of oyster larvae that have been linked to ocean acidification (Feely et al. 2010). These mortalities have occurred despite the existence of several eelgrass flats and fringes in the bay where the hatchery is located. In Dabob Bay, my model estimates that seagrass production can reduce DIC by 13.75 to 23.54 μmol kg^{-1} and change pH by 0.03 to 0.05 units (Table 4). These results suggest that carbon draw-down from seagrass production alone will be insufficient to completely offset effects of ocean acidification.

While *Z. marina* exhibits net uptake of carbon and has the potential to influence local carbonate chemistry, the capacity for substantial draw-down of carbon at the scale of basins or sub-basins appears limited. Although my calculations estimate that carbon assimilation rates are on the order of 10^{10} gC y^{-1} for Puget Sound Basin, and range from 10^{8} to 10^{10} gC y^{-1} for the sub-basins, *Z. marina* beds only occupy approximately 3.7 to 4.5% of the total surface area of the Puget Sound basin and are mainly restricted to shallow coastal waters. It is unlikely that a sufficiently large fraction of seawater in the Puget Sound basin, or in any sub-basin, would come in contact with *Z. marina* long enough to significantly alter the carbonate chemistry of the water body. This would suggest that the capacity for a basin wide effect is improbable and that any change in carbonate chemistry due to eelgrass metabolic processes is more likely to be observed at highly localized scales.

Field validation of my results clearly is called for. Even so, the estimates of carbon draw-down reported here are generous. Local carbonate chemistry can be significantly influenced by terrestrial inputs (Doney et al. 2007, Borges and Gypens 2010), which are not well quantified for the Puget Sound region (Feely et al. 2010). These added influences are important to note, because the majority of Puget Sound's shorelines and eelgrass habitats are adjacent to areas of urban and sub-urban development. Moreover, a proportion of the carbon assimilated by seagrasses that is not buried in the sediments or exported from the system will be re-released into the water column through microbial decomposition of detritus. Although the quantity of carbon re-released through decomposition is not well established, it is clear that not all of the carbon assimilated by seagrass will be removed from the system.

My estimates of carbon draw-down were limited to the carbon assimilated by seagrasses through metabolic processes and did not account for production and respiration by other members of the seagrass community. In seagrass systems dominated by *Z. marina*, seagrass accounts for the largest fraction of carbon assimilated from seawater. However, other community members including epibionts and other benthic organisms can significantly alter net ecosystem production and thereby influence local carbonate chemistry. For example, algal epibionts living on leaves of *Z. marina* assimilate carbon for use in photosynthesis, thereby potentially adding to local draw-down of carbon. However, because these epibionts tend to be short-lived, much of the carbon they assimilate is labile and likely re-released to the water column over days or weeks. Moreover, epibionts slow the growth of the host plant, thereby reducing carbon assimilation by *Z. marina*. Heterotrophic organisms living in association with *Z. marina* also will influence rates of carbon draw-down. For example, measurements of net primary productivity in Chapman Cove, WA by Thom et al. (1994) were consistently negative because the rate of respiration by the benthic community exceeded photosynthetic rates. Net-heterotrophic systems such as this would not exhibit a net draw-down of carbon from the local environment.

Burial in sediments is perhaps the most effective natural way of sequestering seagrass-assimilated carbon over the long term. However, only a fraction of the carbon assimilated by seagrass is effectively buried. In studies of seagrasses in the tropics, Duarte et al. (1998) estimated that 50-60% of seagrass production is put directly into the sediments through seagrasses roots and rhizomes. This below-ground material is not likely to be exported out of the system but instead is buried in sediments over long periods of time, potentially exceeding millenary time scales if left undisturbed (Romero et al. 1992, Pergent et al. 1994, Mateo et al. 1997). Comparable estimates have not been made for *Z. marina* in the Puget Sound region. Even so, applying the 60% burial rate estimated by Duarte et al. (1998) to my estimates of carbon assimilation yields a rate of carbon burial that is small relative to the magnitude of the OA problem.

Carbon can be exported from seagrass beds through transport of detrital materials. A fraction of the carbon assimilated by seagrass is stored in the above-ground biomass (i.e., leaves) and when this biomass is 'turned-over,' there is potential for some of this carbon-containing detritus to be exported from the immediate seagrass system and into deeper waters where it can be buried or otherwise sequestered. Some studies (Thom 1990, Valiela 1995) suggest that seagrasses have a high production to mean annual biomass (P:B) ratio, possibly as high as 300, which means that the seagrass biomass is replaced from one to 300 times annually; this makes the potential export of carbon assimilated by seagrasses very high. According to Kennedy et al. (2010), there is evidence of seagrass carbon found buried in sediments tens of meters away from seagrass meadows, suggesting a potential export from the system. On the west coast of North America where submarine canyons are close to shore, seagrass detritus exported from shallow beds can be trapped at depth (Vetter and Dayton 1998). A study by Thom et al. (2001) suggests that export of seagrass detritus occurs within and beyond Puget Sound, based on observations of large quantities of seagrass-associated carbon in deep portions of Puget Sound and in open water in offshore areas of Washington State.

I estimated the draw-down potential under current environmental conditions, recognizing that in a changing climate these estimates are likely to change. Several studies, including those by Thom (1990) and Thom et al. (2003) have already attributed fluctuations in eelgrass abundance to large climate anomalies such as El Nino and La Nina events. As the climate changes, physical drivers such as increased sea surface temperature or increased sedimentation could inhibit the ability of *Z. marina* to photosynthesize efficiently, thereby inhibiting the ability of the eelgrass to function as a carbon draw-down unit (Zimmerman et al. 1997, Thom et al. 2001). For example, Hood Canal, which includes Dabob Bay and supports numerous shellfish farms, is located in a sub-basin in which sea surface temperatures are expected to increase significantly and impacts of ocean acidification are expected to be high (Feely et al. 2010). Because respiration generally increases with temperature, increased water temperatures could diminish the ability of the eelgrass to remove carbon from the system. Alternatively, a number of studies have noted that seagrasses, including *Z. marina*, are likely to be competitively dominant under high CO_2 conditions. In elevated CO_2 experiments, Palacios and Zimmerman (2007) demonstrated increased productivity by *Z. marina*. The broader literature supports the idea that seagrasses likely will show positive responses to elevated CO_2 conditions which is consistent with projections for terrestrial C3 species (Duarte et al. 2011, Koch et al. 2013). A study of Puget Sound eelgrass by Thom (1996) indicated that *Z. marina* is, in fact, carbon limited and that an increase in dissolved carbon would likely result in increased growth.

In addition to community respiration and long-term climatic changes, several other variables could influence the results I obtained. For simplicity, my analysis assumes that NPP is constant throughout the year. However, Thom et al. (2008) has demonstrated that NPP varies seasonally. I used only summer estimates of NPP to match data from DNR and to quantify carbon draw-down when NPP is at its maximum in the Puget Sound region (Thom et al. 2008). Plant densities within *Z. marina* beds is also likely to affect draw-down capacity. I was unable to quantify this differences based on density because plant density is not measured as part of the SVMP data set. Finally, my analyses and the Unsworth et al. (2012) model both assume a 'static system' where the surrounding seawater does not move to or from the seagrass bed within the dilution period. Adding a dynamic component could influence the resultant estimates.

My findings suggest that *Z. marina* has limited utility as a tool to ameliorate local effects of ocean acidification in Puget Sound. At some sites, for example Padilla Bay, *Z. marina* can assimilate enough carbon to offset a substantial fraction of the anthropogenic carbon derived from the atmosphere, but it is not yet clear whether *Z. marina* can draw-down enough carbon to have a biologically meaningful effect in this system. Clearly, empirical evidence is needed to test the results of the model I presented. In the meantime, the call to preserve native seagrass beds remains relevant. Seagrasses provide numerous ecosystem services and contribute to the resilience of marine systems in Puget Sound. Their loss reduces scope for adaptation to marine environmental change in both the natural and human systems.

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