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Comparison of non-native dwarf eelgrass (*Zostera japonica*) and native eelgrass (*Zostera marina*) distributions in a northeast Pacific estuary: 1997–2014

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Abstract: In this study, we investigated the rate and pattern of expansion of a non-native eelgrass, *Zostera japonica*, in relation to the distribution of the native eelgrass *Zostera marina* in a coastal estuary of the northeastern Pacific Ocean. The distributions of the *Zostera* congeners were monitored between 1997 and 2014 in Yaquina Estuary on the central Oregon coast, USA, using digital classification of color infrared aerial photographs and ground surveys. Correction factors for seasonal variations in cover were obtained to normalise the annual photo survey results to a common date (mid-August). Major expansions in the distributions of *Z. japonica* meadows over most of the 17-year study period were observed. However, there was no indication that the large (~1500%) increase in areal extent of *Z. japonica* in the lower estuary between 1997 and 2007 was accompanied by a change in areal extent of the native *Z. marina* in this system.

Keywords: estuary; expansion; northeastern Pacific; *Zostera japonica*; *Zostera marina*.

Introduction

Major concerns in environmental management are the modes of introduction, rates of expansion and ecological effects of non-native species (Ruiz et al. 1997, Vitousek et al. 1997, Wonham 2003). Examples of aquatic ecosystems are numerous and include the introduction of marine algae such as *Caulerpa taxifolia* (Vahl) C. Agardh into the Mediterranean Sea (Boudouresque and Verlaque 2002), the zebra mussel (*Dreissena polymorpha* Pallas, 1771) into the Great Lakes (Berkman et al. 1998) and the green crab (*Carcinus maenas* Linnaeus, 1758) into northeastern Pacific coastal waters (Carlton and Cohen 2003, Yamada et al. 2005). In the latter region, another non-native species of concern is the dwarf eelgrass *Zostera japonica* Aschers. *et* Graebn., which generally occurs above the mean lower low water (MLLW) datum in the intertidal zone of estuaries in the Pacific Northwest (PNW), USA (Harrison 1982, Thom 1990, Young et al. 2008, Ruesink et al. 2010). A specific concern is that the introduction and expansion of this non-native species might affect the native eelgrass *Zostera marina* L., possibly reducing the distribution and abundance of this benthic angiosperm, which is generally considered to be a foundation species in temperate coastal estuaries of the Northern Hemisphere (Orth et al. 2006, Ruesink et al. 2010, Short et al. 2011, Orth and McGlathery 2012). From an earlier study in Yaquina Estuary, Larned (2003) reported that accurate measurements of *Z. japonica* cover were not available, and Kaldy (2006) supported this observation, commenting that there was little data on the distribution, seasonality and spread of *Z. japonica* in PNW estuaries. The major objective of this report is to describe, over the 17-year interval 1997–2014, the rate and pattern of expansion of *Z. japonica* in comparison to that of the native eelgrass *Z. marina* in this ecosystem.

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Background

Zostera japonica and *Z. marina*

The dwarf eelgrass *Zostera japonica* was introduced to PNW coastal estuaries more than 50 years ago, apparently with the importation of seed oysters (*Crassostrea gigas* Thunberg) used in the mariculture industry (Phillips and Shaw 1976, Harrison 1982, Posey 1988). *Zostera japonica* first was reported in Willapa Bay, Washington in 1957 (Posey 1988), and nearly 20 years passed before its first observation in Yaquina Estuary, Oregon, in 1976 (Bayer 1996). Harrison (1982) studied seasonal and annual variations of *Z. japonica* in lower British Columbia, Canada, and other studies of this species in PNW estuaries subsequently have been reported (below). In recent years a number of investigations of the occurrence and ecology of *Z. japonica* in Yaquina Estuary have been published (Specht et al. 2000, Larned 2003, Kaldy 2006, Almasi and Eldridge 2008, Young et al. 2008, Shafer et al. 2011, Kaldy and Shafer 2013, Shafer and Kaldy 2014, Shafer et al. 2014).

Seagrasses have long been considered to constitute critically important habitats in coastal and estuarine ecosystems (Orth 1973, Jackson et al. 2001, Green and Short 2003), and *Zostera marina* is the dominant seagrass of the northeastern Pacific (Phillips 1984). There has been great concern expressed regarding the loss of seagrass habitats world-wide (Short and Wyllie-Echeverria 1996, Hemminga and Duarte 2000, Orth et al. 2006, Orth and McGlathery 2012, Short et al. 2014). Whether there is evidence of a loss of *Z. marina* in PNW estuaries has been a question posed by marine ecologists over the last decade (Borde et al. 2003, Kentula and DeWitt 2003, Thom et al. 2003, Gaeckle et al. 2011, Young et al. 2012). Similarly, there has been growing interest in the expansion of the non-native *Z. japonica* in these estuaries (Kaldy 2006, Shafer et al. 2008, Young et al. 2008, Mach et al. 2010, Ruesink et al. 2010, Kaldy and Shafer 2013, Shafer et al. 2014, Kaldy et al. 2015).

Aerial photography – digital orthophotography for benthic habitat mapping

At our laboratory, research into the distribution of eelgrasses in Yaquina Estuary began in 1997. We utilized aerial photography with false color near-infrared (color infrared, CIR) film, which we found provided substantially better contrast between vegetated and unvegetated sediment than full color film (Young et al. 1999). To provide training for the photo interpreter, an extensive ground survey of vegetated and unvegetated intertidal habitats in the estuary was conducted (described below). A detailed method of orthorectifying diapositive prints from the CIR film and classifying the intertidal vegetation target habits also was developed (Clinton et al. 2000, 2007). Aerial photography surveys were conducted annually (spring or summer) between 1997 and 2007, with modifications of the procedures as described elsewhere (Young et al. 1998, 2008, 2010, 2012, Specht et al. 2000). Results and interpretations of the 11 aerial surveys are discussed here, as well as results of ground surveys conducted through 2014.

Materials and methods

Study area

Yaquina Estuary is a drowned river valley on the central Oregon coast (Figure 1). Head of tide is approximately 42 km to the east of the mouth, and the average lagoon depth is 3 m below mean sea level (MSL). The estuarine water surface area is 16 km^2 at mean high water (MHW) and 10 km^2 at mean low water (MLW) (Percy et al. 1974). The intertidal area consists of 2.2 km^2 of tidal flat and 3.3 km^2 of salt marsh (Northwest Area Committee 2005). The semi-diurnal tidal range is 3 m, with a tidal prism volume of 24×10^6 m^3, and the average runoff is 9.6×10^8 m^3 (State Water Resources Board 1965). The study area discussed here and shown in Figure 1 includes a large majority of the intertidal and near-subtidal *Zostera marina* distribution in the entire estuary. Our aerial photo surveys over the years indicate that more than 96% of the total area classified as intertidal/near-subtidal *Z. marina* between the estuary mouth (river km 0) and the city of Toledo (river km 20) occurs within this zone.

Aerial photography and image classification

We obtained and processed aerial photographs for 11 annual surveys made between 1997 and 2007. Initially the

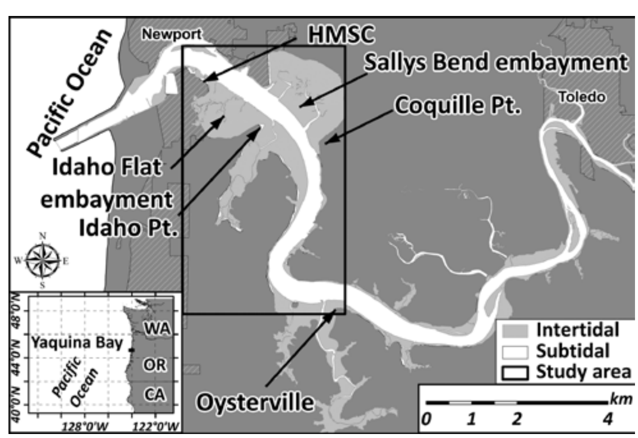

Figure 1: Study area in Yaquina Estuary, Oregon, USA.

surveys were conducted in mid-summer (July and August), presumed to be the period of maximum cover. However, at this time, spectral interference from benthic macroalgal blooms interfered substantially with the efforts to classify intertidal and near-subtidal distributions of *Zostera marina* (Young et al. 2008), and monthly ground surveys provided percent cover data that enabled normalization of the classifications to a common date. Thus, after 1999, priority was given to late spring aerial surveys, weather permitting. The surveys were conducted during daylight hours under tidally exposed conditions (<0 m relative to the MLLW datum) with CIR film (Kodak Aerochrome, Eastman Kodak Co., Rochester, NY, USA). A large-format (23×23 cm) camera equipped with a forward-motion-compensating stabilized mount and a 152-mm or 305-mm focal length calibrated lens was used (Zeiss RMK Top 15, Z/I Imaging GmbH, Aalen, Germany). Details of the annual aerial surveys are presented (Table 1). Descriptions of the procedures used for image classification have been provided elsewhere (Clinton et al. 2007, Young et al. 2008, 2010, 2012). It is important to note here that our technique cannot distinguish spectrally between distributions of the two congeners. However, as discussed below, over the course of this study *Zostera japonica* has been observed to occur in the upper intertidal zone, whereas *Z. marina* has been observed in the lower intertidal zone of the study area. At any one location, the two distributions routinely have been observed to be separated by a significant extent of unvegetated sediment. This fact enabled the photo interpreter to distinguish between images of the two congener distributions and to classify them separately in lower Yaquina Estuary.

Table 1: Dates of the aerial surveys of Yaquina Estuary and times the photography was initiated.

Year	Date	Time[a] (a.m)	Tidal range[b] (m)	Photo-scale	Ground pixel (m)	Digital scanning
1997	07/23	10:04	1.42	7200	0.25	Diapositive
1998	08/10	9:29	1.79	6000	0.25	Diapositive
1999	07/15	10:01	0.89	7200	0.25	Diapositive
2000	08/02	10:09	0.18	7200	0.25	Diapositive
2001	05/09	9:35	0.13	7200	0.25	Diapositive
2002	8/11	9:48	0.63	7200	0.25	Diapositive
2003	8/1	9:52	0.25	10,000	0.25	Diapositive
2004	04/09	9:26	0.09	10,000	0.25	Diapositive
2005	7/21	9:00	0.11	20,000	0.25	Film
2006	5/16	10:03	0.05	20,000	0.25	Film
2007	07/05	10:57	0.14	19,500	0.25	Film

Also shown are changes in tidal elevation during a given survey and survey photoscales, as well as pixel sizes of the digital orthorectified photographs and the media scanned during the digitation process. [a]Pacific daylight time; [b]Relative to MLLW datum.

Ground surveys

1997 Calibration survey

When the aerial photography program began in the summer of 1997, ground-training data were obtained from non-random quadrat surveys. During July, numbered stakes were placed at arbitrarily selected stations in various benthic habitat classes. For each class, three patches were selected at each of six locations, extending over a range of 6 km between the Hatfield Marine Science Center (HMSC) and Oysterville in the lower estuary (Figure 1). Then, a 0.5×0.5 m quadrat with two orthogonal sets of five strings was placed in the four compass quadrants around a stake, and percent cover was measured using the point-intercept method (Greig-Smith 1964). The locations of the station stakes were positioned using a differentially corrected global positioning system – DGPS, Model CMT PC5-L (Corvallis Microtechnology®, Corvallis, OR, USA). The percent cover values obtained at the ground stations in the estuary then were used for training in the classification process developed by the photo interpreter. Georectification accuracy of the 1997 digital orthophotographs (photoscale 1:6000) was determined by locating in the photographs ten photo visible geodetic survey points distributed across the study area. These positions then were used to obtain root mean square error (RMSE) offset values from the published geodetic survey point positions (Clinton et al. 2007).

Seasonal surveys

Between June 1999 and May 2003, surveys of *Zostera marina* percent cover values were conducted in 33×30 m intertidal zones in the upper sectors of *Z. marina* meadows in Idaho Flat and Sallys Bend embayments, near Idaho Point and Coquille Point, respectively (Figure 1). Three survey lines parallel to the channel and 10 m apart were established in the center of each 1000-m^2 zone. For each line of a given survey, three positions between 1 m and 33 m along the line were obtained from a table of random numbers and, using the point-intercept method at each position, percent cover was determined from a quadrat alternately placed 1 m upslope or downslope of the survey path. These surveys were conducted approximately twice per month in late spring and summer and once or twice per quarter in late autumn and winter.

Monthly averages of percent cover values for the combined embayments were obtained to provide a basis for normalizing the total areas of *Z. marina* cover from the image classifications to a common month of comparison (mid-August). In addition, a method of conducting a DGPS mapping of eelgrass meadow boundaries from a hovercraft (Young et al. 2008) was used on three *Z. japonica* meadows in Sallys Bend embayment between April 2011 and November 2012. These results were used for a corresponding normalization of the image classifications of this eelgrass congener extent to mid-August.

2004 and 2007 Random position surveys

An assessment of the accuracy of our classifications of *Zostera marina* and unvegetated sediment habitats first was conducted during April and May 2004. Using photographs of the intertidal zone obtained during the springs of previous years, this zone first was divided into these two strata. Following the procedure described by Congalton and Green (1999) and using a random number generator, 100–200 locations within each stratum were determined and enumerated. A sub-meter DGPS, Model GeoXT (Trimble, Inc.®, Sunnyvale, CA, USA) was used to navigate sequentially to most of these stations, which then were surveyed for percent cover of *Z. marina* using the point-intercept method. However, to reduce discrepancies between the results of the ground survey and the image classifications owing to positional errors, the size of the quadrat used in the four compass quadrants around a point was increased to 1.25×1.25 m. Also, by surveying in the spring before the summer bloom of benthic macroalgae, significant interference from such blooms in the classification of *Z. marina* distributions was avoided. Approximately 20% of the stations from each stratum were randomly selected for training purposes in the photo interpretation; data for the remaining stations were not viewed by the photo interpreter until the classifications had been completed. Spatial accuracy for the rectification of the 2004 digital aerial photographs was assessed by comparing 14 RMSE offset values for positions of photo visible objects in the orthophotographs (photoscale 1:10,000) referenced to published National Geodetic Survey positions (Young et al. 2012).

During summer 2007, using the procedure described above, a series of randomly determined positions within *Z. japonica* meadows and unvegetated sediment strata was obtained. The same method as used for the 2004 *Z. marina* survey was followed, except that percent cover values within the quadrats were estimated independently by two observers and then averaged. The average deviation from the mean of such paired observations above 10% cover was 11±2% (95% confidence interval, CI). The 2004 ground survey results for *Z. marina* were used again to assess the accuracy of the 2007 *Z. marina* classifications. Macroalgal interference in the classification of the distributions was judged to be insignificant. Spatial accuracy of the 2007 digital orthophotographs was determined from a mean for 12 RMSE offset values obtained from orthophotographs (photoscale 1:20,000) of another Oregon coastal estuary (Coos Bay) surveyed in 2005 (Young et al. 2012).

Bathymetric distributions and habitat areas by river km zones

The classifications obtained for the 1997 and 2007 aerial distributions of *Zostera marina* and *Zostera japonica* in lower Yaquina Estuary were overlaid on a bathymetric distribution model (Young et al. 2012). Distance and areal data were obtained by overlay of a distance raster that emulated the distances water would travel with our *Zostera* spp. classification rasters.

1997–2012 Change analysis surveys

In summer 2012, the sub-meter DGPS was used to navigate to a given station of the summer 1997 survey, where percent cover values again were obtained using a 0.25×0.25 m quadrat in the four compass quadrants and the point intercept method. This was the same procedure used in the 1997 survey; the 2012 data then were compared, station by station, to the 1997 percent cover values in a change analysis.

Results

Spatial accuracy

The mean (±95% CI) of ten RMSE offset values for positions of photo visible objects in the 1997 aerial orthophotograhs (photoscale 1:6000), relative to published positions of corresponding geodetic survey points, was 0.49±0.23 m (Clinton et al. 2007). For the 2004 aerial photography survey (photoscale 1:10,000), the mean of 14 RMSE offset values was 0.72±0.27 m. A similar analysis for 12 RMSE offset values obtained from the 2005 orthophotography of Coos Bay, OR (photoscale 1:20,000) yielded a mean offset of 0.99±0.38 m (Young et al. 2012).

Classification accuracy

Following the procedures and definitions described by Congalton and Green (1999), the results obtained from the image classifications were compared via classical confusion matrices to those from the 2004 and 2007 ground surveys for percent cover of the target *Zostera* species (Table 2). In this comparison, the characterization of a given station as “*Zostera* spp.” or “bare substratum” habitat from the ground (reference) survey is accepted as correct. Then for a given class (e.g. *Zostera japonica* from the 2007 survey), the producer’s accuracy (61%) is the number of stations for which there is classification agreement (22) divided by the total number of stations classified from the reference survey (22+14=36). Alternatively, the user’s accuracy for that class (92%) is the number of stations for which there is classification agreement (22) divided by the total number of stations classified from the image classification (22+2=24). In comparison, for the 2004 and 2007 surveys of *Zostera marina* the producer’s accuracy was 98% and 90%, respectively, whereas the user’s accuracy was 98% and 88%, respectively.

To assess the effectiveness of this classification procedure, values for the Kappa index KHAT (and their estimated 95% CI) for these matrices also were calculated as a measure that assesses improvement over chance (Fielding and Bell 1997). The values for the two *Z. marina* surveys were 0.945±0.002 and 0.73±0.08, respectively. For *Z. japonica*, the index was 0.61±0.17.

Comparisons of *Zostera marina* and *Z. japonica* image classifications

The best-fit polynomials to the seasonal cover or extent values for *Zostera marina* (Figure 2) and *Zostera japonica* (Figure 3) were used to normalize all the areal extent values from the image classifications to August 15 (Julian Day 227). A map of the July 2007 normalised areal distributions *of Z. marina* and *Z. japonica* obtained from the image classifications is presented (Figure 4), along with the location of the “river km” positions in the lower estuary. For the 581 ha of intertidal flat in the study area, the 2007 classifications of these congeners indicated that 18.7% of the intertidal zone was *Z. marina* habitat, and 3.2% was *Z. japonica* habitat. Using the modelling approach described above, the areal extents (ha) of these two congeners for 0.5-km wide sectors of the estuary in 1997 and 2007 also are illustrated (Figure 5). The data in these figures were used to obtain values for the area-weighted average distance from the estuary mouth in 1997 and 2007 for *Z. marina* (5.05 and 5.08 km, respectively) and *Z. japonica* (5.52 and 5.59 km, respectively).

Table 2: Accuracy assessments for the image classifications of intertidal *Zostera marina* and *Zostera japonica* vs. unvegetated sediment obtained from aerial and ground surveys of Yaquina Estuary.

	Image class	Reference class		
		Zostera spp.	Bare substratum	User’s accuracy
2004	*Z. marina*	50	1	98%
	Bare substratum	1	27	96%
Producer’s accuracy		98%	96%	
Overall accuracy	97%			
KHAT±95% CI[a]	0.945+0.002			
2007	*Z. marina*	148	21	88%
	Bare substratum	16	101	86%
Producer’s accuracy		90%	83%	
Overall accuracy	87%			
KHAT+95% CI[a]	0.73+0.08			
2007	*Z. japonica*	22	2	92%
	Bare substratum	14	54	79%
Producer’s accuracy		61%	96%	
Overall accuracy	83%			
KHAT+95% CI[a]	0.61±0.17			

[a]Assuming a normal distribution for the Kappa index (KHAT) (Jenness and Wynne 2005).

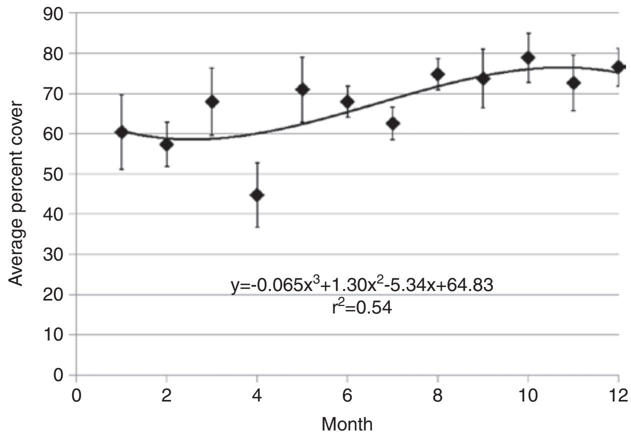

Figure 2: Monthly average values (±95% CI) for percent cover of *Zostera marina* plants within the 1000-m² monitoring zones off Idaho and Coquille Points, obtained from randomly-placed 0.25-m² quadrats (1999–2002).

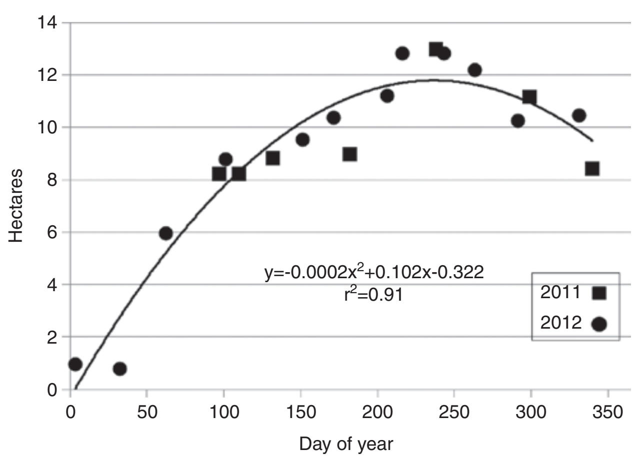

Figure 3: Seasonal variation in area of selected *Zostera japonica* meadows within Sallys Bend embayment, mapped via DGPS from a hovercraft (April 2011–November 2012).

Variation in *Zostera marina* and *Zostera japonica* areal extent and elevation: 1997–2007

Based upon the image classifications obtained from the 11 annual surveys, the total (August normalized) areas of *Zostera marina* and *Zostera japonica* cover in the lower estuary obtained between 1997 and 2007 are presented (Figure 6A and B). No systematic pattern was observed for *Z. marina*; the best-fit linear curve for the data was $y=103-0.20x$ ($r^2<0.01$, $p=0.94$), where "x" is the year surveyed (1 for 1997 and 11 for 2007, Figure 6A). In contrast, a clear trend of areal expansion was obtained for *Z. japonica*; the best-fit exponential curve $y=e^{0.27}x$ was highly significant ($r^2=0.70$, $p<0.0001$), explaining 70% of the variation in the data (Figure 6B). Distributions of the amount of intertidal habitat in the study area at different 0.25-m increments of tidal elevation, and of the percent occupancy of

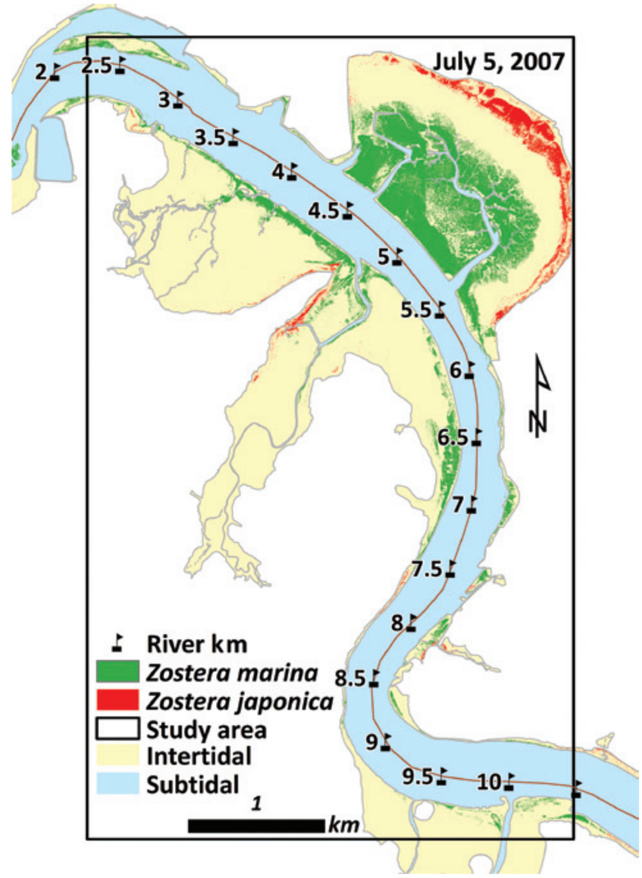

Figure 4: Areal distributions of *Zostera marina* and *Zostera japonica* from classification of digital orthophotographs obtained from the July 2007 aerial survey of lower Yaquina Estuary.

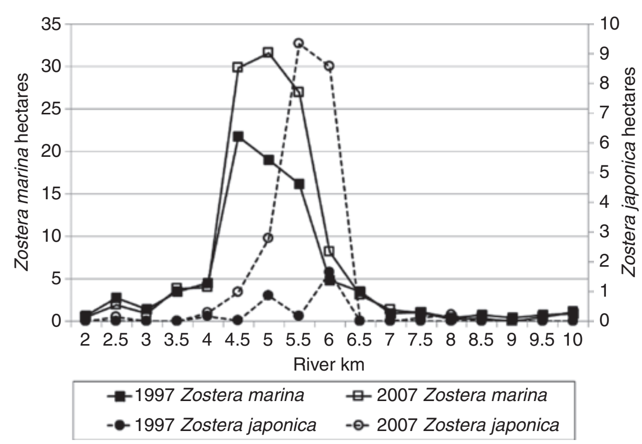

Figure 5: Area of *Zostera marina* and *Zostera japonica* as a function of distance from the mouth of Yaquina Estuary, from August normalised classifications of the digital orthophotographs obtained in 1997 and 2007.

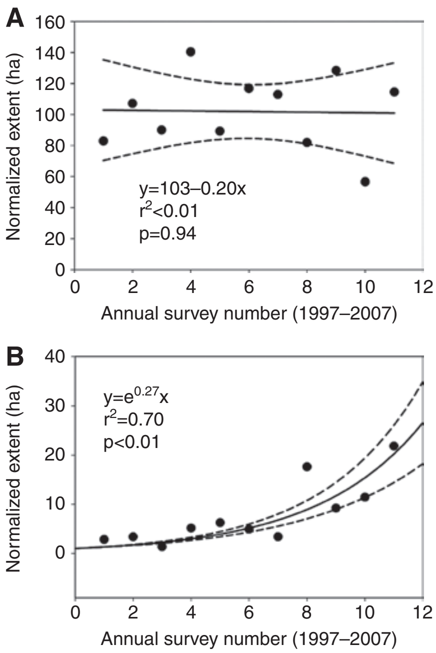

Figure 6: Total (August normalised) area of intertidal *Zostera marina* (A) and *Zostera japonica* (B) in lower Yaquina Estuary from orthophotograph image classifications (Year 1 is 1997, Year 11 is 2007) and best-fit equations with 95% CI.

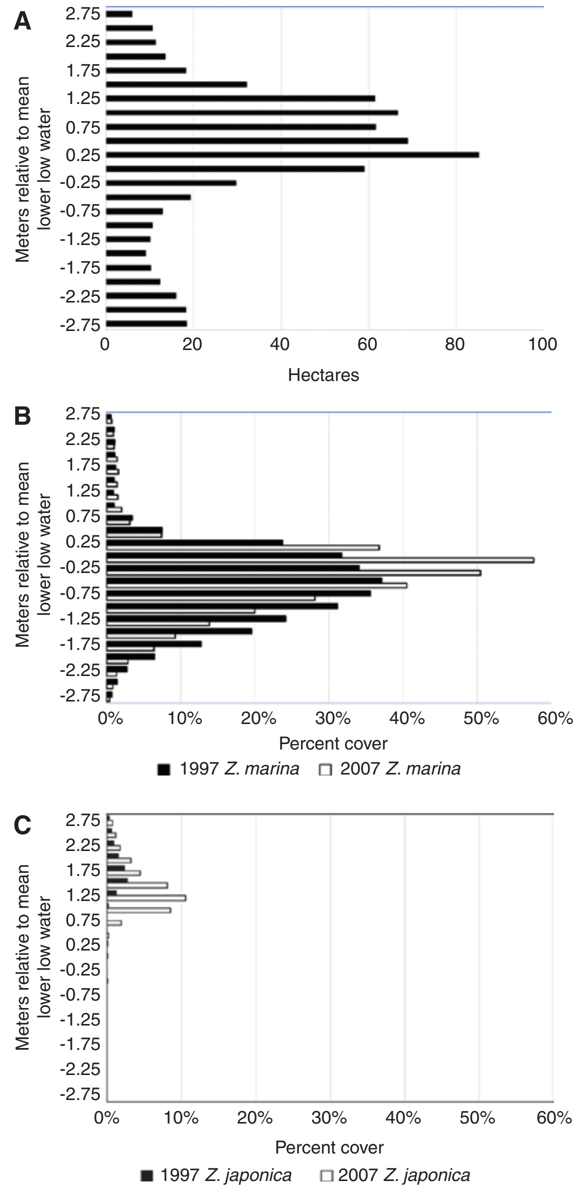

Figure 7: Frequency distributions at 0.25-m increments of tidal elevation in the study area: area of intertidal habitat (A), and percent occupancy by *Zostera marina* (B) and *Zostera japonica* (C) for 1997 and 2007.

Z. marina and *Z. japonica* in these bands of intertidal area measured at the beginning and end of the aerial survey program, also are illustrated (Figure 7). These data do not indicate a substantial change in the average elevation of the native eelgrass between 1997 and 2007; however, the average elevation of the non-native congener decreased from about 1.6 m to about 1.3 m over the decade.

Zostera marina change analysis: 1997 vs. 2012

Of the approximately 280 stations selected for the aerial photography calibration survey in summer 1997, 162 were re-surveyed during the summer of 2012. For the 102 stations where *Zostera marina* cover was measured during one or both surveys, the native eelgrass occurred at 67 and 81 of these stations in 1997 and 2012, respectively, with average cover values of 39.3±7.2% (95% CI) and 29.3±6.1%, respectively.

Expansion of *Zostera japonica* cover within the Idaho Flat embayment: 2000–2014

The expansion of *Zostera japonica* within the Idaho Flat embayment is illustrated by the comparison of the distributions mapped on foot with a DGPS on June 23, 2000 and August 13, 2014 (Figure 8). The mean of the eight total

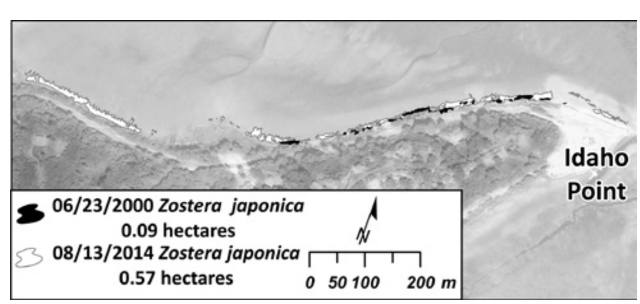

Figure 8: Perimeters of *Zostera japonica* patches in Idaho Flat embayment, mapped via DGPS on foot (June 23, 2000 and August 13, 2014).

percent cover values so obtained between August 2007 and August 2014 was 0.44±0.13 (95% CI) ha, four times the value obtained in June 2000 (0.11 ha).

Discussion and conclusions

Spatial and classification accuracy

The aerial photography rectification techniques used for this study have provided orthophotographs with spatial accuracies within 1.4 m at a 95% confidence level. These results are well within the national mapping standards for spatial accuracy of 2.5 m and 5.0 m RMSE at respective photoscales of 1:10,000 and 1:20,000 (US Geological Survey 1996).

The KHAT values (Table 2) are a measure of how well the remotely sensed classification agrees with the reference data (Congalton and Green 1999). Landis and Koch (1977) characterized the possible ranges for KHAT into three groupings: a value between 0.80 and 1.00 represents strong agreement; a value between 0.40 and 0.80 represents moderate agreement; and a value below 0.40 represents poor agreement. Based upon these criteria, our KHAT results for the 2004 and 2007 classifications of *Zostera marina* (0.94 and 0.73) represent strong and moderate agreement, respectively, whereas that for the 2007 classification of *Zostera japonica* (0.61) represents moderate agreement. The lower value for *Z. japonica* may result from the fact that the relatively small size of the blades of this dwarf eelgrass and their propensity to be mixed with surficial sediment during exposed conditions on the tidal flats, confound the distinction between *Z. japonica* and bare substrate classifications from the digital orthophotographs.

Seasonal variation of *Zostera marina* and *Z. japonica* cover values

The best-fit annual curve for monthly averages of percent cover in the two embayments obtained for *Zostera marina* (Figure 2) suggests a summer-to-winter ratio of about 1.3. This value is similar to those obtained for shoot density in PNW estuaries by Harrison (1987), Thom (1990) and Ruesink et al. (2006). Substantially greater seasonal variation in areal distribution was measured for *Z. japonica* in Sallys Bend embayment of Yaquina estuary, as indicated by the best-fit curve (Figure 3). The total area within the perimeters of the target meadows mapped during midsummer (July–August) exceeded that measured in winter (January–February) by about a factor of 12. This is consistent with the results of other studies that document a nearly complete leaf loss of *Zostera japonica* during winter months (Harrison 1982, Thom 1990, Baldwin and Lovvorn 1994, Kaldy 2006, Ruesink et al. 2006).

Eelgrass variation with distance from estuary mouth

The comparison of areas of cover by *Zostera marina* and *Zostera japonica*, in 0.5-km sectors of the lower estuary over the decade (Figure 5), shows no change in area-weighted average distance from the estuary mouth for either congener. This clearly is a result of the geomorphology of the study area, which is dominated by the two large embayments (Idaho Flat and Sallys Bend) situated about 4–6 km from the mouth (Figure 1). The greatest distributions of the two congeners are found in these shallow embayments (Figure 4), with relatively large areas where the bathymetry supports the two distributions of intertidal eelgrass (Young et al. 2008, 2012). As mentioned above, no significant overlap in the distributions has yet been observed in lower Yaquina Estuary (Kaldy 2006, Young and Specht, unpublished data). This pattern is typical of that found in most of the estuaries of the Pacific Northwest; Shafer (2007) summarised zonation classifications of sites in Canada, Washington, Oregon and California, concluding that overlap of the two congeners occurred in only 5 of the 16 systems examined.

Annual variation in areal extent and average elevation

The comparison of August normalized areal extent values (ha) of *Zostera marina* and *Zostera japonica* in lower Yaquina Estuary shows distinctly different temporal trends. For the native eelgrass, no significant change between 1997 and 2007 was observed (Figure 6A). In contrast, for the non-native dwarf eelgrass, a systematic temporal increase in extent is implied (Figure 6B). The best-fit exponential equation yielded an areal expansion from about 1.3–19 ha over the 10-year interval, an increase of approximately 1500%. This major expansion is reflected in the distinct decrease in the average elevation (above the MLLW datum) of the *Z. japonica* distribution in the lower estuary, from about 1.6 m in 1997 to about 1.3 m in 2007 (Figure 7). Since in 2007, approximately 86% of the classified *Z. japonica* occurred in Sallys Bend; this appears to be the main location of the down-slope expansion.

As discussed above, the results of the 2012 re-survey of 162 of the stations selected as part of the 1997 image interpretation training exercise, despite some variability, do not indicate a substantial change in the proportion of stations with *Z. marina* over the 15-year interval. This is consistent with the results of the aerial surveys of the extent of *Z. marina* conducted between 1997 and 2007. These findings indicate that, during this period of the major *Z. japonica* expansion in lower Yaquina estuary, conditions required for the maintenance of the overall distribution of the native eelgrass there were relatively stable.

However, several studies have shown that the abundance of *Z. marina* at specific locations in the estuary can vary over time as a result of disturbance or natural stress. Boese (2002) investigated the effect of recreational clam harvesting on eelgrass there, where approximately 10% of the eelgrass is subjected to this activity. He observed statistically significant reductions of the above- and below-ground biomass of *Z. marina* 1 month after his clam-digging treatment, and the trend for reduced abundances was still apparent after 10 months. Subsequently, Boese et al. (2005) observed that *Z. marina* plants growing in the high intertidal zone had significantly lower above-ground biomass per shoot compared to those growing in the low intertidal zone. The authors attributed this to increased desiccation stress from exposure at higher elevations. They commented that this kind of acute desiccation stress is often observed in late spring and early summer when daytime spring-tides and sunny and windy weather combine. Thus, differences in desiccation stress over time could cause variability in the abundance of the native eelgrass at a given site. Other evidence of local stress was reported in a 2001–2002 study of the effect of erosion and macroalgal accumulation on eelgrass distribution in the estuary (Boese and Robbins 2008). For example, two steeply sloped plots were partially washed out when a natural intertidal drainage channel changed location on the tidal flat and, in another plot, the deposition of woody debris damaged the perennial eelgrass. Elsewhere, a small perennial patch died out for unknown reasons. Finally, Boese et al. (2009) investigated the recolonization rate of *Z. marina* following experimental removal of shoots and rhizomes, such as can occur from propeller scarring of the substrate by grounded boats. They reported that bare areas near the centers of their experimental plots were still bare up to 30 months after the removal treatment, and that recovery occurred by new shoots originating from rhizomes growing in from plot edges. As part of this study, changes in a propeller scar (106×1 m) caused by a 1998 grounding were monitored in four of our aerial photo maps made between 1997 and 2003. The authors concluded that eelgrass recolonized the scar at a linear growth rate of ~0.5 m per year. These studies show that variability in the abundance of native eelgrass on small temporal and spatial scales can occur in the estuary, consistent with our findings from the comparative ground surveys of 1997 and 2012.

In contrast to the down-slope expansion of *Z. japonica* observed in the lower estuary, dominated by the south-oriented Sallys Bend distribution, for the north-oriented Idaho Flat distribution, the expansion of this non-native eelgrass was in the along-shore direction only. Recently, Kaldy et al. (2015) have provided evidence that increased duration of exposure to cold water temperatures may limit expansion of the lower boundary of *Z. japonica* into the mid-intertidal zone. On the basis of this finding, Kaldy (personal communication) has suggested that mid-intertidal temperature differences, driven by differences in sun exposure between the two embayments, may be a cause of the different patterns of expansion of *Z. japonica* observed in these two sub-systems of the lower Yaquina Estuary. This hypothesis requires further investigation.

Ecological and management implications

One ecological implication of the findings of this study is that no association was obtained between the large (~1500%) expansion in areal extent of *Zostera japonica* in lower Yaquina Estuary between 1997 and 2007 and the extent of its native congener *Zostera marina* in the lower intertidal zone over this period. Thus, any ecological effects of this expansion should be limited to the upper-to-mid intertidal zone. Although this was not a topic of investigation in our study, the subject has been examined by numerous researchers over the years (Harrison 1982, 1987, Posey 1988, Larned 2003, Bando 2006, Kaldy 2006, Ruesink et al. 2006, Mach et al. 2010, Ruesink et al. 2010, Lamberson et al. 2011), and an extensive summary recently has been provided by Shafer et al. (2014). These authors also summarised the management implications of the spread of this non-native eelgrass in estuaries of the Pacific Northwest.

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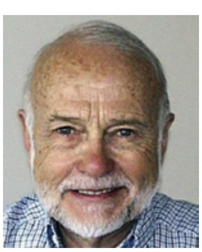
Bionotes



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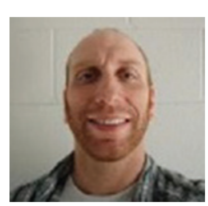

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