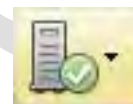# WILEY
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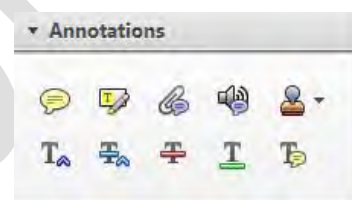
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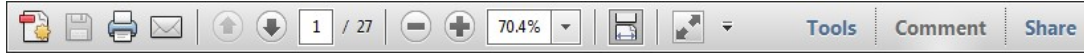
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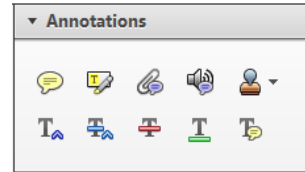
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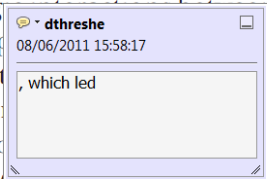### 1. Replace (Ins) Tool – for replacing text.

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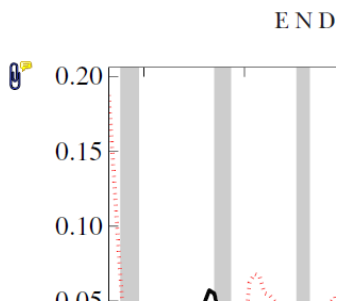
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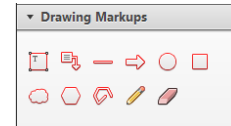
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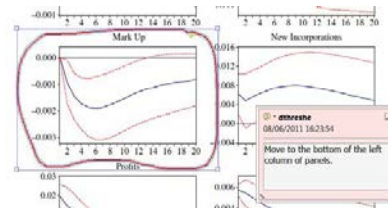
Forty years of seagrass population stability and resilience in an urbanizing estuary

Andrew O. Shelton[1,2]*, **Tessa B. Francis**[3], **Blake E. Feist**[1], **Gregory D. Williams**[4], **Adam Lindquist**[5] and **Philip S. Levin**[1,6,7]

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Summary

1. Coasts and estuaries contain among the most productive and ecologically important habitats in the world and face intense pressure from current and projected human activities, including coastal development. Seagrasses are a key habitat feature in many estuaries perceived to be in widespread decline owing to human actions.

2. We use spatio-temporal models and a 41-year time series from 100s of km of shoreline which includes over 160 000 observations from Puget Sound, Washington, USA, to examine multiscale trends and drivers of eelgrass (*Zostera* spp.) change in an urbanizing estuary.

3. At whole estuary scale (100s of km), we find a stable and resilient eelgrass population despite a more than doubling of human population density and multiple major climactic stressors (e.g. ENSO events) over the period. However, the aggregate trend is not reflected at the site scale (10s of km), where some sites persistently increase while others decline.

4. Site trends were spatially asynchronous; adjacent sites sometimes exhibited opposite trends over the same period. Substantial change in eelgrass occurred at the subsite (0·1 km) scale, including both complete local loss and dramatic increase of eelgrass.

5. Metrics of local human development including shoreline armouring, upland development (imperviousness) and human density provide no explanatory power for eelgrass population change at any spatial scale.

6. Our results suggest that the appropriate scale for understanding eelgrass change is smaller than typically assumed (approximately 1- to 3-km scale) and contrasts strongly with previous work.

7. *Synthesis.* Despite ongoing conservation concern over seagrasses world-wide, eelgrass in Puget Sound has been highly resilient to both anthropogenic and environmental change over four decades. Our work provides general methods that can be applied to understand spatial and temporal scales of change and can be used to assess hypothesized drivers of change.

Key-words: coastal development, eelgrass, Puget Sound, Resilience, shoreline armouring, spatio-temporal models, urbanization, *Zostera*

Introduction

Nearly 40% of the world's population lives within 100 km of a coast (Sale *et al.* 2014), most of the world's major cities are located in coastal zones (Timmerman & White 1997;

Small & Nicholls 2003), and future population expansion will increase disproportionately in the world's coastal zones (Seto, Güneralp & Hutyra 2012; Sale *et al.* 2014; Neumann *et al.* 2015). Human development and activities in coastal regions place enormous stress on natural systems and have negatively affected the structure and function of many nearshore and coastal ecosystems (Imhoff *et al.* 2004; Lotze *et al.* 2006;

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Greene *et al.* 2015). Anticipating and adapting to such changes requires an understanding of where and when such human activities occur, the mechanisms driving change in coastal ecosystems, and the spatial and temporal scale at which change is occurring (Rahbek 2005).

Of particular importance in coastal marine ecosystems are foundational, habitat-forming species (Dayton 1972) like mangroves, saltmarshes and seagrasses that support productive marine communities. Seagrasses, in particular, play a vital role in temperate and tropical coastal marine systems, providing habitat for species of conservation concern (Heck *et al.* 2008), supporting fisheries (McArthur & Boland 2006; Orth *et al.* 2006), providing coastal protection and erosion control (Koch *et al.* 2009; Arkema *et al.* 2013), mediating ocean carbon chemistry (Fourqurean *et al.* 2012), improving water clarity (Gacia, Granata & Duarte 1999; Lee & Dunton 1999) and providing subsidies to other marine ecosystems (McGlathery *et al.* 2012). As the ecosystem functions provided by seagrasses have become increasingly appreciated over the past decade (Barbier *et al.* 2011), concern over both the threats to and population trajectories of seagrasses has grown (Orth *et al.* 2006; Waycott *et al.* 2009; Short *et al.* 2011).

Threats to seagrasses are well documented (Orth *et al.* 2006; Grech *et al.* 2012). On large spatial scales threats include increased ocean temperature and changing ocean chemistry (Koch *et al.* 2013; Thomson *et al.* 2015) while localized threats include light limitation from overwater structures, sediment loading, and eutrophication associated with development and agriculture (Gallegos & Bergstrom 2005; Li *et al.* 2007; Rehr *et al.* 2014), direct disturbance from dredging, aquaculture, and fishing (Simenstad & Fresh 1995; Short & Wyllie-Echeverria 1996; Cardoso *et al.* 2010), and threats from shoreline modifications (Patrick *et al.* 2014; Patrick, Weller & Ryder 2016). In addition to these bottom-up drivers, top-down drivers have been identified recently as potentially playing an underappreciated role in seagrass population dynamics (Heck *et al.* 2000; Williams & Heck 2001). Top-down drivers include both direct herbivory on seagrasses (Hughes & Stachowicz 2004), and direct and indirect effects of meso-grazers on seagrass communities (Heck *et al.* 2000; Duffy *et al.* 2015).

Nearly all threats to seagrasses are positively correlated with human population density and activities. Waycott *et al.* (2009) synthesized global seagrass time series to show a persistent global loss of seagrasses since at least 1940 (median annual loss rate between −0·29% and −0·84% annually; their Table S2, Supporting Information) and asserted that negative impacts on seagrasses due to humans were accelerating. While such global averages provide large-scale descriptors of seagrass trends, there is substantial variation in seagrass trends at local and regional scales (Waycott *et al.* 2009). Furthermore, both the drivers of seagrass change and management actions to increase, maintain or recover seagrass populations often occur at regional or local scales. Thus, detailed studies on local seagrass populations are required to link trends to environmental and anthropogenic drivers. To date, a major hindrance to understanding seagrass systems has

been a lack of long-term monitoring data (Duarte 2002). As seagrass beds can persist over long periods of time and may respond to an array of factors that act on a range of spatial and temporal scales (from the scale of metres to 100s of km, and days to decades), understanding seagrass drivers and trends requires data collected across appropriate spatial and temporal scales.

Here, we focus on understanding trends and drivers of eelgrass (*Zostera* spp.) populations in an urbanizing estuary in the north-east Pacific. We develop and apply novel statistical methods to understand large-scale spatial and temporal changes in eelgrass populations. We incorporate over 160 000 observations that span more than 500 km of shoreline and 41 years (1972–2012) to provide one of the only large-scale and long-term descriptions of seagrass habitats in the north Pacific. We document eelgrass change at regional and local scales and consider the role played by both regional and local drivers in generating trends. We extend available information about Puget Sound eelgrass by nearly 30 years (see WDNR 2015) and summarize eelgrass trends at three scales: regional (100-km scale), site (1–10 km) and local (0·1 km). We utilize a diverse suite of spatially explicit environmental and human covariates to ask how changes in shoreline and water attributes at regional, site and local levels contribute to changes in eelgrass. Additionally, our time series spans a wide range of well-documented environmental changes including several major ENSO events (1982–1983, 1988–1989, 1997–1998 and 2010–2011; Clarke 2014). The spatial and temporal signatures of eelgrass change allow us to begin to disentangle the drivers of eelgrass populations in Puget Sound and provide actionable information for practitioners working to maintain and recover seagrasses both in Puget Sound and temperate systems world-wide.

Materials and methods

STUDY AREA AND SPECIES

All sampling was conducted in Puget Sound, a large fjord-like estuary in the southern portion of the inland Salish Sea (Fig. 1). Puget Sound covers an area of approximately 2330 km^2 at low tide (Burns 1985) with an average depth of 150 m and a maximum depth of nearly 300 m. Circulation is driven by tidal currents, seawater inflow from marine waters, freshwater outflow from rivers and winds (Ebbesmeyer & Barnes 1980; Thomson 1994). Human populations are concentrated on the eastern shore of the central basin around the commercial ports of Seattle, Tacoma and Everett and 60% of the state's population lives within 20 km of the Puget Sound coast (Appendix S2).

We focus on the native eelgrass *Zostera marina*. Eelgrasses are the most abundant temperate species of seagrass, occurring along the coasts of the north Pacific Ocean from Japan to Mexico and widely in the north Atlantic Ocean. Eelgrass beds generate considerable ecological and economic value (Irlandi, Ambrose & Orlando 1995; Costanza *et al.* 1997; Plummer *et al.* 2013), providing spawning substrate and nursery habitat for numerous fish and invertebrates (Heck & Thoman 1984; Heck, Hays & Orth 2003), and fuel primary production and detrital pathways in nearshore food webs (McConnaughey & McRoy 1979; Valentine & Heck 1999). Furthermore, eelgrass is frequently used as an indicator of the function of nearshore marine
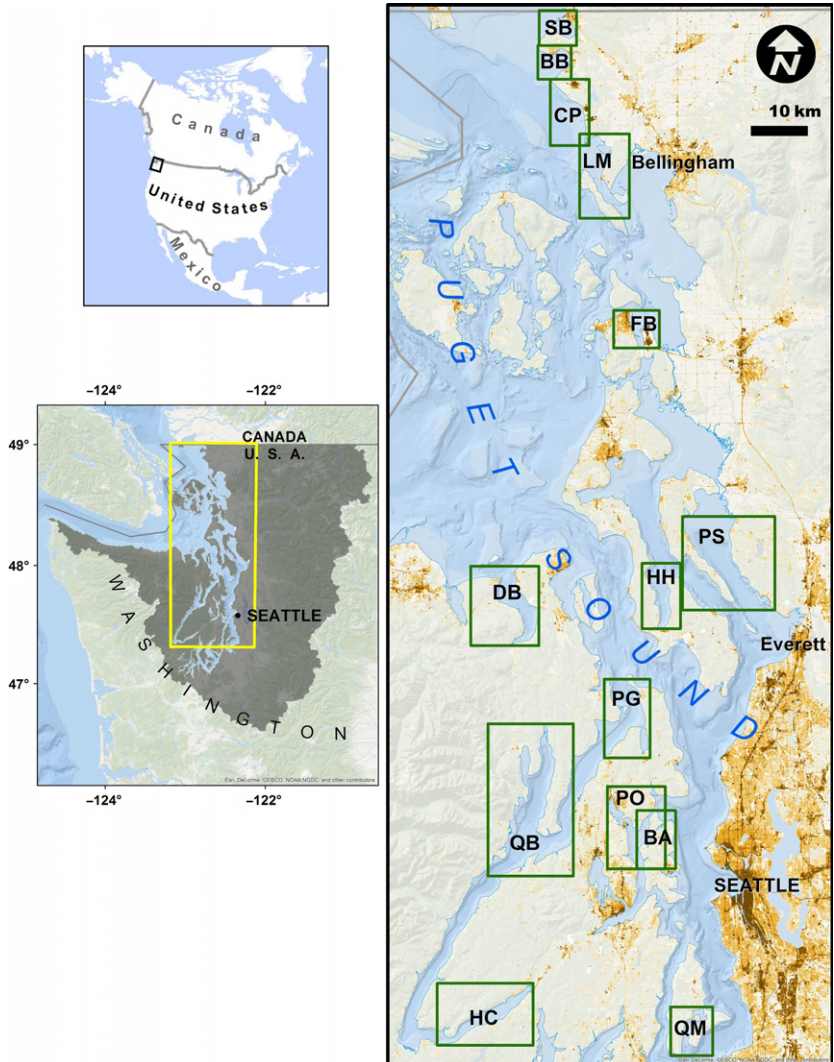
Fig. 1. Puget Sound study area and focal areas included for examination of eelgrass trends. Boxes with two letter identifiers are used throughout the paper. Grey shading in bottom left panel delineates watershed areas that drain into Puget Sound. Yellow, orange and brown colours identify impervious surfaces with darker colours indicating higher proportion imperviousness. [Colour figure can be viewed at wileyonlinelibrary.com]

ecosystems (Partnership 2011). As with seagrasses world-wide, there are few long-term descriptions of eelgrass populations, or seagrasses in general, in the north Pacific (Duarte 2002).

In 2015, the native eelgrass *Z. marina* covered approximately 20 000 ha in Puget Sound (WDNR 2015), where it grows in muddy to sandy habitats in intertidal and shallow subtidal zones. Shoot density may reach 800 shoots per m^{-2} and shoot length may exceed 2 m (WDNR 2015).

SURVEYS AND DATA

We use information gathered during herring spawning surveys conducted by the Washington Department of Fish and Wildlife (WDFW) to document nearshore habitat change within Puget Sound between 1972 and 2012. During herring spawning season in Puget Sound [January–March for all sites but Cherry Point (CP) which occurs in April–June; Fig. 1], WDFW personnel survey nearshore spawning habitats by dropping a specially designed metal rake (a modified grappling hook) to the shallow nearshore benthos from a small boat, ensnaring benthic vegetation and retrieving the rake. For each rake sample, the geographic coordinates, presence of 29 benthic vegetation categories (most identified to genera), abundance category of herring eggs on vegetation and water depth are recorded. During a single survey, samples are collected approximately every 200 m along the

coast, though the frequency varies substantially by site and across years. Sampling occurs at all tidal stages and at depths from mean sea level to c. 10 m below mean sea level. Approximately weekly surveys are conducted at each survey location, resulting in hundreds to thousands of georeferenced observations at each spawning location in each year (Trumble *et al.* 1977; Stick 1994; Stick, Lindquist & Lowry 2014). Across all sites and years this data set includes more than 250 000 unique, georeferenced observations spanning 41 years.

For this article, we focused exclusively on the most commonly observed vegetation category, *Zostera* spp. (eelgrass; almost exclusively *Z. marina*, though very rarely *Zostera japonica* may be observed). As we were primarily interested in detecting temporal trends and spatial patterns in eelgrass occurrence, we restricted our analyses to sites that had extensive temporal and spatial sampling coverage; we included sites first sampled in 1980 or earlier and had at least 4000 observations across the entire time series. This resulted in 160 932 observations from 11 survey locations for our analyses (Table S1.1).

We used the data from surveys to generate trends for 14 sites of comparable size (representing between 12·5 and 27·0 km of shoreline; Fig. 1, Table 1); we divide the shoreline of the Cherry Pt. survey into four sites to make them comparable in size to other sites (SB, BB, CP and LM are derived in part from the Cherry Pt. data). Similarly data from surveys at Port Orchard-Port Madison were divided into

Table 1. Summary of trend areas

Site	Herring survey location	Length of shoreline (km)	Area eelgrass (ha; time series mean)	Area eelgrass (ha; 2011–2012)	Total potential area (ha)	Mean proportion eelgrass cover (2011–2012)
SB	Semiahmoo Bay	15·1	841	876	977	0·896
BB	Semiahmoo Bay and Cherry Point	12·5	550	651	890	0·731
CP	Cherry Point	14·7	108	78	474	0·164
LM	Cherry Point	27·3	1023	1154	1463	0·789
FB	Fidalgo Bay	14·5	731	672	896	0·750
DB	Discovery Bay	27·0	199	169	322	0·525
HH	Holmes Harbor	20·1	279	290	294	0·986
PS	Port Susan	21·6	172	229	386	0·593
PG	Port Gamble	20·6	235	202	359	0·563
PO	Port Orchard-Port Madison	22·2	167	151	412	0·366
BA	Port Orchard-Port Madison	22·1	84	58	313	0·185
HC	South Hood Canal	11·2	365	369	456	0·809
QB	Quilcene Bay	18·2	242	238	336	0·708
QM	Quartermaster Harbor	26·9	179	183	476	0·384
	Sum	**274·0**	**5,176**	**5,321**	**8,055**	
	Among-site mean					**0·661**

comparably sized sites: PO and BA. Site SB is surveyed by two different surveys (one in the late winter, one in the late spring as part of the Cherry Pt. survey), but is only counted as one site, resulting in a total of 14 trend sites.

As most survey locations had missing data – all but one had at least 1 year in which no rake samples were collected – and to ease computation, we binned observations data into 2-year groups (e.g. we combined data from 1974 and 1975). Combining data into 2-year groups had the effect of halving the number of spatial fields estimated by the model, greatly sped model estimation and produced metrics of model fit. We explored alternate binning strategies using 4-, 5- or 10-year bins, but preliminary comparisons of models showed that 2-year bins provided the best combination of statistical tractability and model fit.

To examine spatial and temporal changes in eelgrass, we divided the shore into 100-m-long segments and assigned covariate values for each 100-m-long segment. Each observation was associated with the nearest shoreline segment based on Euclidean distance. This approach acknowledges positional uncertainty about the location of individual observations – sampled locations were not identified using GPS until the 2000s and earlier locations were digitized from hand drawn charts. Additionally, this approach reflects the uncertainty about how terrestrial anthropogenic covariates are connected to specific subtidal locations.

To account for spatial and temporal sampling variation, we only estimated trends in eelgrass for shore segments that had sufficient numbers of observations (≥ 3 observations within 0·5 km) in at least 10 of the 20 possible 2-year time periods. Thus, only shore segments with observations spanning at least 20 years were used to describe trends. Because the first year of data varies among sites (Table S1.1), we estimated eelgrass occurrence for all sites beginning in 1981–1982, and thus, we present the total area of eelgrass for 1981–1982 to 2011–2012.

STATISTICAL ANALYSES

To understand changes in eelgrass, we constructed spatio-temporal statistical models of eelgrass occurrence for each survey location. The model provides estimates of eelgrass occurrence at a fine spatial and temporal scale at each site that can be aggregated to produce a picture of eelgrass change in Puget Sound at multiple spatial and temporal scales. We model the presence or absence of eelgrass for observation i in time t at shoreline segment s, $Y_{it}(s)$, using a binomial generalized linear mixed model (GLMM) with a logit link. Let $p_{it}(s)$ represent the probability of occurrence at segment s in year t, $X_{it}(s)$ represent a matrix of fixed covariates (described below), β represent regression coefficients estimated for each covariate, and $\varepsilon_t(s)$ represent spatio-temporal random effects, then,

$$Y_{it}(s) \sim \text{Bernouli}(p_{it}(s)) \qquad \text{eqn 1}$$

$$\text{logit}(p_{it}(s)) = X_{it}(s)\beta + \varepsilon_t(s).$$

Thus, the occurrence of eelgrass is described by the contribution of measured environmental covariates as well as a random effect to include the contribution of unmeasured – but potentially spatially and temporally varying – covariates. We provide alternative model structure for incorporating shared trends across shoreline locations in Appendix S1. Furthermore, we note that the model structure employed is extremely general and flexible and can be used to account for a wide variety of model structures (see also Cressie & Wikle 2011).

This statistical approach assumes that the eelgrass collected by the rake provides a statistically unbiased sample of the presence of eelgrass. While we have no data about the sampling efficacy of the rake itself, it is possible that it either over- or under-represents the true occurrence of eelgrass. Therefore, while we present estimates of occurrence and total eelgrass area, these estimates may by biased by an unknown constant of proportionality. Since the same equipment and methodology have been used for all sites and the entire times series, this effect will be constant across our entire data set, making comparisons within and among sites appropriate. Thus, while absolute estimates of abundance may be statistically biased, estimates of trend are unaffected.

COVARIATES

We included five continuous covariates as fixed effects in our model. The first, water depth (m), was recorded during the survey and is

available for each observation (Appendix S2). We expect an optimum depth to be associated with eelgrass distributions and thus include both linear and quadratic terms (depth and depth^2) as covariates. Since we do not have the time at which measurements were taken, we cannot adjust recorded depths relative to a standard tidal datum (e.g. mean low water), and so we used the reported depth. The resulting observation error in the water depth measurements likely introduces uncertainty in our estimates of the effect of depth on eelgrass occurrence.

We evaluated the effect of four additional covariates on eelgrass, focusing on physical attributes of, and anthropogenic modifications to, nearshore habitat hypothesized to influence eelgrass presence and distribution. We included two physical attributes important to seagrass: wave exposure (Stevens & Lacy 2012) and bathymetric slope (Koch 2001), measured as distance to the 5·48 m (3 fathom) isobaths (Appendix S2). We included two anthropogenic covariates: the proportion of shoreline that is armoured (bulkheads, riprap, concrete walls, etc.) and the mean imperviousness (a general proxy for human development) of a 150-m buffer zone nearest each shoreline segment (Appendix S2). As with the rake survey data, we assigned covariate values to each 100 m shoreline segment. Both armouring and impervious cover variables were fixed values for the entire time series; information about changes to armouring and impervious surfaces in Puget Sound not available across the time series in adequate spatial or temporal detail for this analysis, and used values represent covariates c. 2005 (Shipman 2008; Simenstad *et al.* 2011). Additional anthropogenic covariates were initially considered, but available time series for proxies of likely stressors like eutrophication or sedimentation were unavailable. Publicly available information on marine water characteristics such as nitrate, chlorophyll *a*, phosphate and other nutrients in Puget Sound begin in 1999 (PSEMP 2015) and unavailable for earlier years. As Puget Sound is a marine-dominated estuary, humans contribute proportionally less to marine nutrients than in many other estuarine systems (Steinberg *et al.* 2010; Mohamedali *et al.* 2011; Cope & Roberts 2013).

To evaluate possible site-wide change in eelgrass across time, we also estimated model that included fixed offsets for each time period. We estimated models both with an intercept for each time as well as a model with a single, shared intercept.

To reduce colinearity of the covariates, we centred the distance to the 5·48 m isobath (3 fathom, hereafter 'bathymetric slope') and weighted wave exposure (hereafter 'fetch') covariates before estimation and square-root-transformed fetch to reduce the statistical leverage of extremely large values.

SPATIO-TEMPORAL RANDOM EFFECTS

In eqn 1, the random effect $\varepsilon_t(s)$ represents a vector of spatio-temporal effects at time t and shoreline segment s, and accounts for processes not included in the fixed covariates. To match the structure of available covariates and improve computation, we used the shoreline to provide a one-dimensional background for the random effects. Thus, points that are proximate (either in space or time) will be more strongly correlated than points that are further apart. We write $\varepsilon_t(s)$ as a first-order autoregressive process,

$$\varepsilon_t(s) \sim \text{Normal}(\rho\varepsilon_{t-1}(s), \Sigma) \qquad \text{eqn 2}$$

where ρ defines the strength of temporal autocorrelation and Σ is the covariance matrix that represents spatial covariation in random effects. We constrained ρ to ensure stationarity: $-1 < \rho < 1$. We used a Matérn covariance function with $\nu = 3/2$ to define Σ and estimated fixed effects via maximum marginal likelihood using the Laplace approximation to approximate the integral across random effects (see

Appendix S1). We implemented our model using the R package 'INLA' (www.r-inla.org). To estimate the spatio-temporal random effects, we introduced a knot approximately every 0·5 km of shoreline and used second degree smoothing to describe the spatial field along the shoreline. Further model description and example code can be found in Appendix S1 and in the data archive accompanying this article.

To define the spatial extent of each area, we included shoreline points that were observed regularly during the time series and we included a 0·5-km buffer along the extreme edges of the observed sample points.

MODEL OUTPUTS AND PREDICTIONS

We use the above statistical model for two main purposes. First, from model estimates we made predictions of eelgrass occurrence across all modelled years and combine these predictions to understand temporal changes to eelgrass populations at small (c. 0·1 km) to large (100s km) scales. Secondly, estimated parameters informed the effect of physical and anthropogenic covariates on eelgrass occurrence, and the spatial and temporal scales at which eelgrass respond to unmeasured covariates and stochastic forces.

Since we estimated the model for each survey location independently (11 total), we had eleven estimates for each fixed covariate. We used these eleven estimates to ask how the direction and magnitude of each covariate compared across locations. We also examined estimates of spatial variance and temporal autocorrelation parameters at each site to understand the contribution of unmeasured spatial and temporal effects to eelgrass occurrence.

To predict occurrence, we generated MCMC predictions for the probability of occurrence at the centroid of each 30×30 m grid of cells occurring with shallow coastal waters of Puget Sound. As the area in each grid cell is 900 m^2, the estimated area of eelgrass area for MCMC sample g at time t and location s is $900p_t^g(s)$. The eelgrass area at each site is simply the sum across all grid cells. We produced predictions for a depth range from 0 to 6 m below mean low water at each site in each time period. We made 1000 predictions for each grid cell in each time period and used these predictions to calculate eelgrass trends and bound uncertainty about the trends. In total, we generated predictions for 554·3 km of shoreline representing 13 543 ha of benthic habitat (see Data Archive for a GIS data-base of spatial predictions).

We focus on understanding patterns of eelgrass change at three scales. Starting at the largest scale, we combine information from the 14 trend areas in Puget Sound to produce aggregate measures of eelgrass trend at the scale of hundreds of km of shoreline. Because some areas were not first surveyed until 1981, we provide aggregate estimates of eelgrass only for the period 1981–1982 to 2011–2012. We express our uncertainty for the total Puget Sound area as the sum of individual site variances (estimates for individual trend areas are approximately normally distributed).

At the scale of tens of km scale, we assessed eelgrass and asked whether trends varied within Puget Sound. We estimated linear trends for each site using ordinary least-squares regression on the predicted time series and express the change at each site as a percentage change in area relative to the time series mean of area present at each site. We also used available GIS information to ask whether trends in eelgrass related to site-wide measures of anthropogenic change. We regressed the eelgrass population growth rate against two measures of human impact: the cumulative proportion of shoreline armoured at each site and the area weighted mean imperviousness for drainages leading into each site (Appendix S2). In addition, we use available

human demographic data to calculate the human population density in the freshwater drainages flowing into each area between 1970 and 2000 and regressed rates of human density change against eelgrass growth (Appendix S2).

Finally, at the 0·1-km scale, we asked whether changes in occurrence were homogeneous site-wide or whether intra-site variability underlied site-level changes. We visualized the distribution of eelgrass occurrence both by making maps to identify areas of change and by constructing frequency distributions of the occurrence of eelgrass across all grid cells within each site. To contrast time periods, we compared early (mean occurrence for each grid cell for available years before 1984) and recent (mean occurrence between 2009 and 2012) occurrence. For frequency distributions, we generated probability distributions of eelgrass occurrence using a Gaussian kernel smoother with a bandwidth of 0·02.

Results

We estimated eelgrass occurrence at a fine spatial and temporal scale in 11 Puget Sound survey locations and generated predictions about changes in eelgrass and associated environmental and human covariates for 14 sites of comparable size. Hereafter, we present result for sites in order from north to south to enhance the ability to detect geographic patterns in the results (Fig. 1).

The sites can be classified into two groups: sites where eelgrass has never been abundant (CP, PO, BA, QM; time-average of eelgrass probability of occurrence <0·4) and the remaining 10 sites where more than half of the area is covered by eelgrass on average (Table 1). While the shoreline lengths are relatively similar among sites, the bathymetry of Puget Sound results in substantial variation in subtidal area among sites; each site represents between 294 and 1463 ha of area used for determining trend (Table 1). Taken together, this means that sites do not contribute equally to the total area examined in our study. Estimated eelgrass area ranged from a maximum estimate of 1154 ha in 2012 (LM) to only 58 ha (BA).

AGGREGATE AND LOCAL TRENDS OF EELGRASS

Across 274 km of shoreline representing 8055 ha used for detecting eelgrass trends, we found remarkable stability in the aggregate eelgrass area across survey areas between 1981 and 2012 (Fig. 2). There was no clear signature of decline in eelgrass; the linear regression estimated eelgrass area was flat over the time series (point estimate of 0·02% annual increase). During this same time period, the human population in counties bordering Puget Sound increased from about 2·63 to 4·45 million (Minnesota Population Center 2011).

However, this aggregate flat trend masks substantial variation among sites (Fig. 3). We identified five sites with negative trends (≤−0·5% annual change; CP, FB, DB, PG, BA; Fig. 3), two sites with strong positive trends (≥0·5% annual change: LM, PS), and the seven sites with annual change between −0·5% and 0·5%. There is no obvious geographic structure to the trend from north to south; indeed, an increasing area is occasionally directly adjacent to a decreasing area (compare LM and CP; Figs 1 and 3).
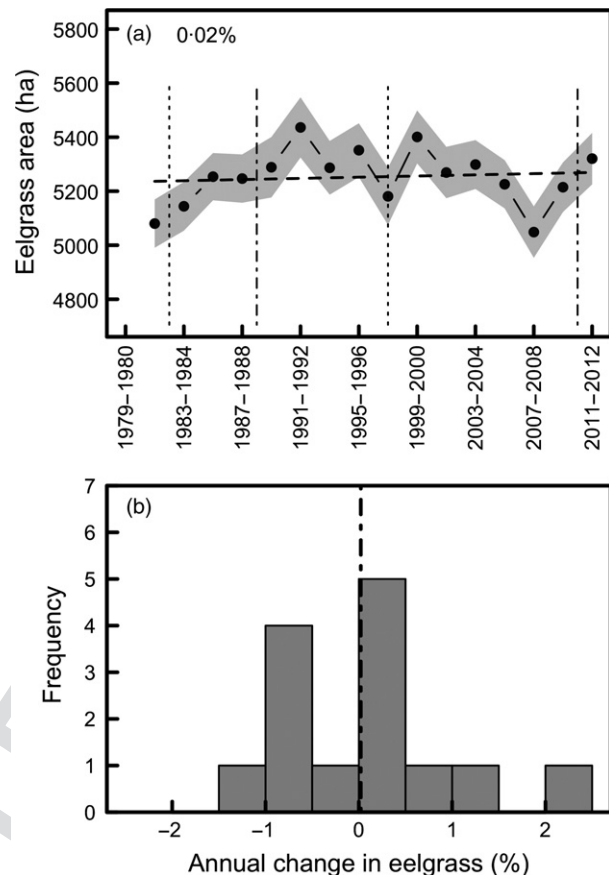

Fig. 2. (a) Cumulative eelgrass area across the 14 trend areas and aggregate trend (annualized per cent area change). Vertical dotted lines indicate major El Niño events (1982–1983 and 1997–1998) and dash-dot lines indicate major La Niña events (1988–1989 and 2010–2011). (b) Frequency distribution of annualized per cent area change. Vertical line indicates estimated cumulative change from the top panel.

COVARIATE EFFECTS

There were varying effects of physical and anthropogenic covariates on eelgrass occurrence. As expected, eelgrass occurrence was strongly negatively associated with water depth (Table S1.3) corresponding to increased light limitation at greater depths. Depth coefficients were strongly negative with all sites having either a negative quadratic (10 sites) or negative linear (one site) effect of depth on eelgrass occurrence (recall that covariate effects are derived for each survey – 11 total – rather than for the 14 trend areas)

Physical variables had no consistent effect on eelgrass occurrence at the 0·1 km scale. Across all areas, most estimated coefficients for fetch overlapped 0, indicating no strong effect on eelgrass (Table S1.3). At two sites (HH, PG) eelgrass had increased occurrence with higher fetch and two sites (CP, QB) had a negative association between fetch and eelgrass. Bathymetric slope had minimal measurable effect on eelgrass occurrence; coefficients for 9 of 11 areas overlapped with zero, one was positive (CP), and one was negative (HH; Table S1.3).

Anthropogenic variables at the 0·1-km scale were also poor predictors of eelgrass occurrence (Fig. S1.2). Shoreline
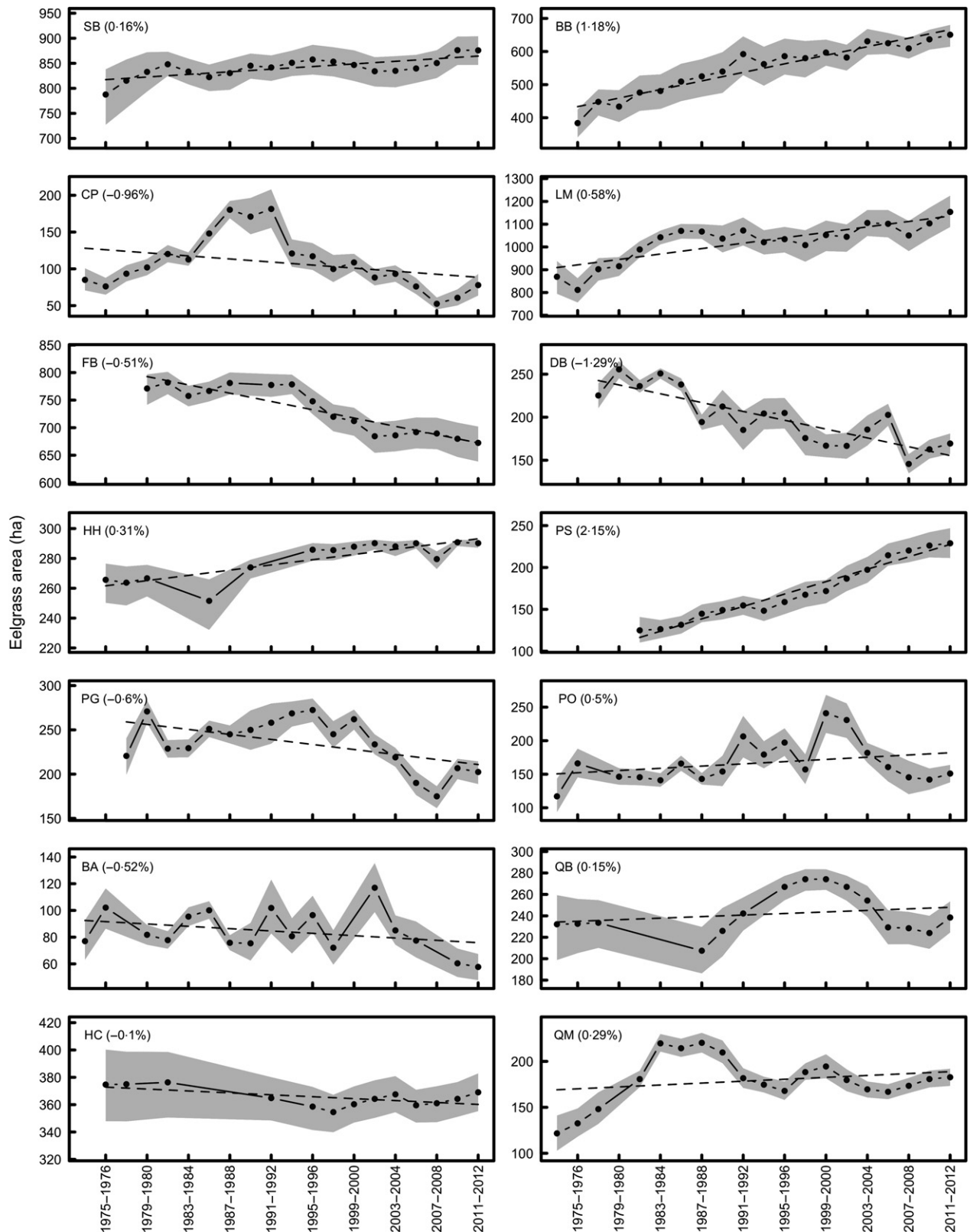
Fig. 3. Time series for each of 14 trend areas. Points and lines indicate mean, shading indicates 95% CI. Dashed line shows linear trend for each site. Note that the *y*-axis varies among panels.

armouring had a negative relationship with eelgrass at 8 of 11 areas but only three had confidence intervals that did not include 0. The magnitude of any armouring effect was small (all slopes are between −1 and 1), suggesting that even if there was a true effect of shoreline armouring on eelgrass, its magnitude was small.

There was minimal evidence of any effect of impervious cover on eelgrass: 9 of 11 sites have coefficients that overlap 0 (Fig. S1.2). The notable outlier was QM with a negative, but highly uncertain, coefficient. Larger coefficients for impervious cover relative to shoreline armouring arise primarily because the range of observed impervious cover was much lower than the range of shoreline armouring (see Fig. S1.1).

Estimates of spatio-temporal random effects $\varepsilon_t(s)$ were often large, indicating a substantial influence of spatial location on eelgrass occurrence. The estimated autocorrelation coefficient (ρ) was >0·90 for all sites but one (Table 2), indicating that the value at a segment at time t was a strong predictor of time $t + 1$. Additionally, the estimated spatial range (the long-shore distance at which the correlation between two points falls to 0·05) was between 1 and 3 km at all sites (Table 2), indicating the spatial scale for factors that may be affecting eelgrass occurrence. For both autocorrelation and spatial range, HH was notably different than the other sites. HH was unique among our sites because there was very little spatial or temporal variation in eelgrass at HH; nearly the entire surveyed area was occupied by eelgrass and this did not change notably over the study period making the spatial field and associated parameters difficult to estimate.

Site-level comparisons of anthropogenic drivers provide no evidence of strong effects of shoreline armouring, imperviousness or change in human density on eelgrass growth (Fig. 4). All examined relationships were not significant though there was a trend towards a negative relationship between human population growth rate and eelgrass population growth rate. This relationship was non-significant and driven by a single site (CP) with a large proportional increase in human density.

IDENTIFYING AREAS OF CHANGE

Above we show minimal change in eelgrass at the level of Puget Sound (100-km scale), but substantial among-site variation (10-km scale). However, site variation was not generally driven by site-wide changes in eelgrass occurrence but rather shifts in occurrence that occur intra-site (0·1- to 1-km scale). We illustrate small-scale changes in occurrence in two ways. First, we provide the distribution of occurrence values for all

Table 2. Estimates of spatio-temporal random effect parameters. Spatial range indicates the long-shore distance at which correlation falls to 0·05

Site	Autocorrelation (ρ)	Spatial range (km)	Spatial variance (σ^2)
BB	0·97 (0·94, 0·99)	2·5 (1·5, 3·9)	3·01 (1·64, 5·50)
CP	0·96 (0·95, 0·97)	1·5 (1·3, 1·8)	2·92 (2·27, 3·66)
FB	0·93 (0·89, 0·96)	1·5 (1·0, 2·4)	2·16 (1·34, 3·52)
DB	0·95 (0·93, 0·97)	1·7 (1·3, 2·3)	2·09 (1·45, 3·01)
HH	0·77 (0·55, 0·92)	9·4 (5·1, 17·8)	2·49 (1·28, 4·99)
PS	0·98 (0·96, 0·99)	2·3 (1·6, 3·4)	2·74 (1·62, 4·78)
PG	0·97 (0·95, 0·98)	1·1 (0·7, 1·6)	2·05 (1·42, 2·98)
QB	0·97 (0·95, 0·98)	1·7 (1·3, 2·3)	4·47 (3·18, 6·34)
PO	0·97 (0·96, 0·98)	2·0 (1·6, 2·5)	4·73 (3·43, 6·62)
HC	0·97 (0·93, 0·99)	1·5 (0·8, 2·4)	1·15 (0·69, 1·93)
QM	0·98 (0·97, 0·99)	3·4 (2·6, 4·5)	7·53 (4·28, 13·89)

of the predicted points on the 30 × 30 m grid for two periods: pre-1984 and 2009–2012 (Fig. 5). For example, sites DB and FB show substantial declines in median occurrence driven by generalized decline in eelgrass occurrence at many locations within the site. BB and PS provide examples of generalized increase in eelgrass. In contrast, while the median occurrence changes only slightly at PG, a substantial portion of the distribution in 2009–2012 is near 1 while another component is very near 0. The near 0 component was not present in the earlier period, indicating that eelgrass has been virtually lost from part of the site. A similar pattern of localized change is evident for BA, QB and QM. Other sites appear very stable (e.g. SB, HH).
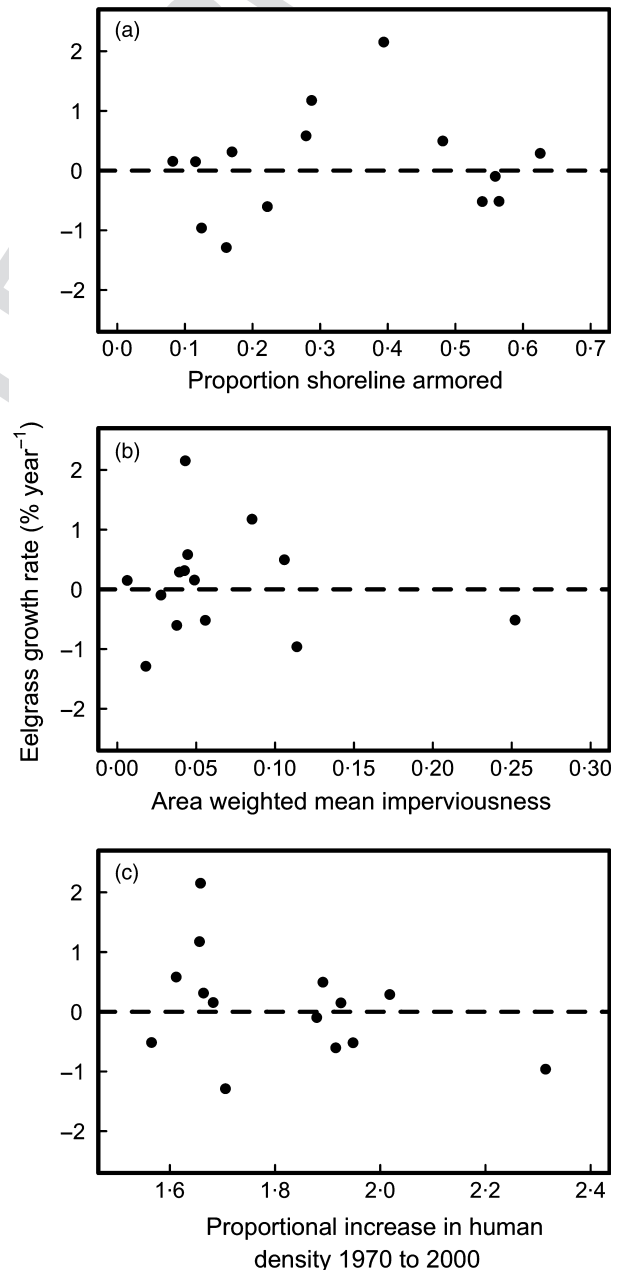

Fig. 4. Relationships between trend area eelgrass growth rate and shoreline armour (a), imperviousness (b) and proportional change in human density (c). Each point represents a trend area.
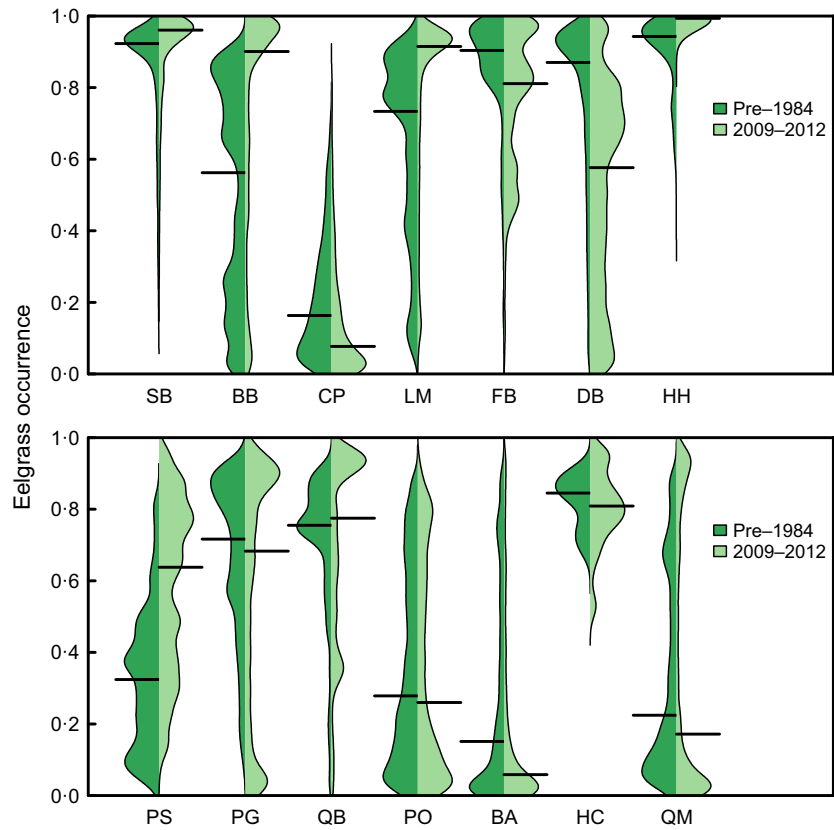
Fig. 5. Distribution of eelgrass occurrence at each site before 1984 (dark green) and in the most recent four years (2009–2012). Shaded areas represent a kernel smoothed probability density of eelgrass occurrence across all grid cells at a site. Grid cells included in the density are identical for each time period and all distributions integrate to 1. Horizontal lines indicate the median occurrence for each probability density at each time period. [Colour figure can be viewed at wileyonlinelibrary.com]

Secondly, we provide maps for three sites to highlight particular areas that have experienced large changes – both positive and negative – over the period (PG, PO, and BA; Fig. 6). We compare predictions from 1981–1982 and 2011–2012. These maps illustrate the patchwork nature of eelgrass bed change in Puget Sound with areas of virtually no change interspersed with areas of both positive and negative change including areas where eelgrass has been entirely lost from stretches of shoreline. We provide figures comparing 1981–1982 and 2011–2012 for the remaining sites in the online supplement (Appendix S3).

Discussion

Seagrasses provide some of the most productive and ecologically significant marine ecosystems in the world, which motivates understanding their status, trend and potential threats (Waycott *et al.* 2009). Seagrass beds thrive in estuarine and nearshore habitats, a nexus of human threats from use and development that are projected to increase in coming decades (Timmerman & White 1997; Seto, Güneralp & Hutyra 2012; Neumann *et al.* 2015). To our knowledge, our analysis presents the longest data set on eelgrass in the north Pacific and among the longest eelgrass time series in the world. It provides an unparalleled opportunity to examine multiscale (both spatial and temporal) trends in eelgrass. Though the data we use were not collected for the purpose of monitoring eelgrass, we feel confident about our conclusions about eelgrass trends in Puget Sound as our basic trends post-2000 match a formal,

stratified eelgrass monitoring programme initiated in the early 2000s (WDNR 2015). Additionally, some specific areas of eelgrass loss identified in our analyses have been previously identified by local experts (Thom *et al.* 2014) and increases confidence in our results.

These results show remarkable large-scale stability in eelgrass across broadly dispersed sites in Puget Sound. This stability occurs despite a rapidly increasing human population (population more than doubled between 1970 and 2010; Minnesota Population Center 2011), multiple major oceanographic anomalies including several major El Niño events (Trenberth *et al.* 2002; Clarke 2014). This stability is also coincident with the implementation of wide ranging of environmental legislation aimed at improving Puget Sound water quality [e.g. Clean Water Act (FWPCA 1972); Washington State Shoreline Management Act (RCW 1971)] and specific protection of eelgrass as a 'habitat of special concern' by WDFW.

Our results have two main general implications. First, and most generally, our work presents general statistical framework for understanding spatial and temporal change in nearshore habitats. While we apply our methods to presence–absence data, the framework is directly applicable to continuous response variables (e.g. plant density), to more complicated two-dimensional spatial problems (Ward *et al.* 2015; Ono *et al.* 2016), and to alternative time series structures. Recent studies have developed various approaches to analysing the spatial distribution of seagrasses (Coles, McKenzie & De'ath 2009; Grech & Coles 2010; March *et al.* 2013; Schubert *et al.* 2015), using remote sensing data to
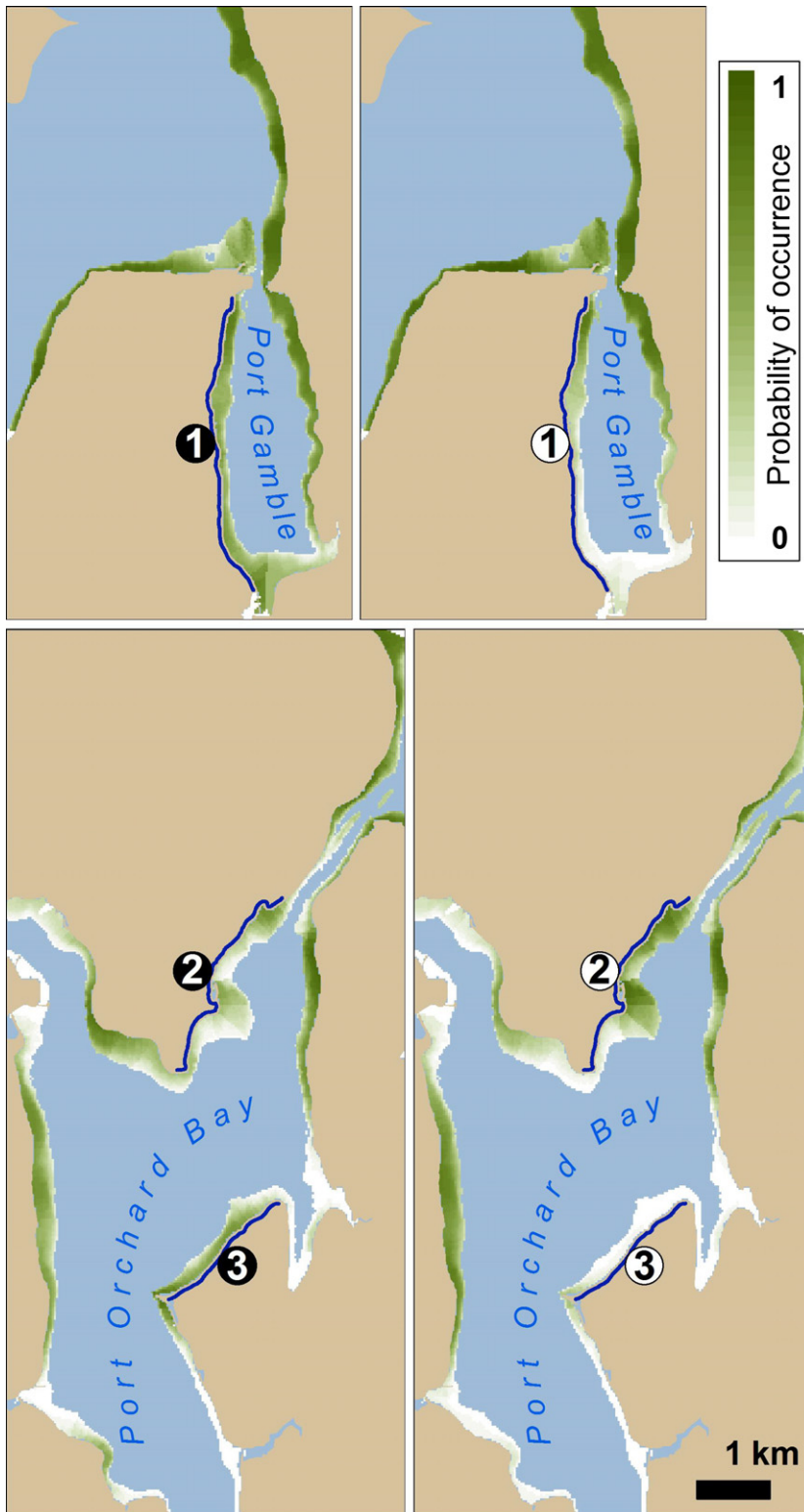
Fig. 6. Estimated mean eelgrass occurrence at sites in Puget Sound in 1981–1982 (left column) and 2011–2012 (right column). The top two panels show Port Gamble Bay (PG), and the bottom shows Port Orchard Bay incorporating parts of site PO and site BA. We make predictions for eelgrass occurrence between mean low water and −6 m. Locations labelled with numbers highlight three stretches with substantial loss (1 and 3) and gain (2) in eelgrass occurrence over the 30 years. Locations above mean low water are coloured in tan, and depths below −6 m are coloured in blue. [Colour figure can be viewed at wileyonlinelibrary.com]

assess spatio-temporal change (Lyons, Roelfsema & Phinn 2013) and projecting seagrass distributions under future climate and development scenarios (Saunders *et al.* 2013), but none to our knowledge has explicitly used spatio-temporal models as we have here. While we were not able to ascribe changes in seagrass to specific measured covariates here, the model identifies locations that have experienced changes during the past 40 years (Fig. 6; Appendix S3). Identified areas of change provide excellent candidates for future studies to elucidate mechanisms underlying the loss or gain of eelgrass and as potential restoration targets.

Our results do not coincide with expected responses of eelgrass to increases in human population size (Orth *et al.* 2006; Patrick *et al.* 2014) whereby light limitation of eelgrass via

algal overgrowth and shading (Burkholder, Tomasko & Touchette 2007) is associated with human presence and increased nutrients (Seitzinger *et al.* 2002). This is likely in part a result of the fjord-like structure of Puget Sound where nutrients are predominantly of oceanic origin and nutrients of terrestrial origin are frequently flushed from shallow nearshore areas (Mackas & Harrison 1997; Steinberg *et al.* 2010). These results also suggest that using aggregate metrics of human impacts, such as impervious surface or human population density in associated watersheds, may not be adequate for assessing the impacts of very localized stressors, such as local nutrient sources or shoreline hardening, on nearshore habitats.

These results do reveal critical information about the spatial scale at which eelgrass responds to the environment. Despite the lack of a detectable signature of shared stressors on eelgrass across sites, research suggests that eelgrass populations are influenced by regional oceanic and climate forces (Brown *et al.* 2013; Valle *et al.* 2014). However, over the past 40 years, eelgrass in Puget Sound has proven resilient to large-scale climatic and anthropogenic change; we do not see coincident changes in eelgrass populations that would indicate a major shared climatic driver across sites (Fig. 3). Instead, our results show that substantial changes to eelgrass populations occur at the site and subsite level. Our sites show no obvious geographic coherence in trends of eelgrass – adjacent sites can have opposite trends – and geographic coherence would be expected if shared oceanographic or climate drivers controlled eelgrass trends. We conclude that the role of local drivers in determining eelgrass persistence is predominant. Our results suggest the relevant spatial scale for evaluating eelgrass change and identifying potential drivers is approximately 1–3 km of shoreline (Table 2).

While we identified locations of significant eelgrass change and identified the appropriate scale for investigating changes, we did not find a clear signature of shoreline armouring or impervious surfaces on eelgrass at scales ranging from 0·1 to 10 km. A major limitation of our covariates were that they were static, reflecting the armouring present c. 2005; no information is available about how these variables changed during the course of our study, potentially leading to underestimates of anthropogenic effects. As most major changes to Puget Sound shorelines long predate 1970 – the ports of Seattle, Tacoma and Everett were developed largely in first decades of the 20th century and likely resulted in large losses of eelgrass – it is unlikely that additional data would radically change our broad scale results. However, we do note that none of our sites include nearshore habitats directly adjacent to dense urban areas like downtown Seattle (Fig. 1) and so we lack information about eelgrass change in response to high levels of urbanization. Eelgrass populations are stable and resilient in the face of substantial changes to the Puget Sound environment over the past 40 years. However, we strongly suspect the development of Puget Sound pre-1970 led to the widespread loss of eelgrass as has been shown in other systems (Serrano *et al.* 2016).

Our work highlights how data on focal species without data on potential pressures of similar spatial and temporal scales can limit the ability to make inference about the drivers of trends. With access to a single snapshot of armouring in Puget Sound c. 2005 (Shipman 2008; Simenstad *et al.* 2011) and time series of land use and land cover that only include the past 20 years (Vogelmann *et al.* 2001; Xian *et al.* 2011; NOAA 2013), no data are available to systematically inform changes of the shoreline before 2000 at the c. 1-km scale. Time series of other potentially important covariates such as nutrient availability and sediments that may affect eelgrass through light availability are similarly unavailable for much of our time frame. This indicates clearly the need for joint monitoring of populations and threats to understand trends in seagrasses, and likely applies to understanding coastal habitats world-wide.

Our results show that despite concerns over the potential for catastrophic, rapid changes in seagrass populations (Orth *et al.* 2006; Waycott *et al.* 2009; Thomson *et al.* 2015), eelgrass population change in Puget Sound is relatively slow and gradual. While very local population declines in Puget Sound have been reported (WDNR 2015) and are hypothesized to be driven by factors ranging from low seedling survival (Dooley *et al.* 2013) to wasting disease (Groner *et al.* 2014), shared, Puget Sound-wide drivers of eelgrass loss are not evident. We do note that because our data are limited to occurrence and do not include density information, our results do not reflect any changes in eelgrass shoot density that may have occurred over the period. We cannot preclude the possibility of future collapses but our analyses suggest that in general management and restoration at the local level can lead to incremental improvements and gradual increases in seagrass populations. Fortunately, as conservation and restoration project implementation largely occur on local spatial scales, our results suggest that localized problems may have local solutions.

Acknowledgements

Data accessibility

Data and GIS files associated with this article are accessible via Dryad Digital Repository, ~~http://dx.doi.org/xxxxx~~ (Shelton *et al.* 2016)

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed description of statistical models and data processing methods.

Appendix S2. Description of GIS methods for deriving physical and anthropogenic variables.

Appendix S3. Comparative maps of eelgrass in 1981–1982 and 2011–2012 for all 14 eelgrass trend areas.

Graphical Abstract

The contents of this page will be used as part of the graphical abstract
of html only. It will not be published as part of main.

Despite ongoing conservation concern over seagrasses world-wide, eelgrass in Puget Sound has been highly resilient to both anthropogenic and environmental change over four decades. Our work provides general methods that can be applied to understand spatial and temporal scales of change and can be used to assess hypothesized drivers of change.

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