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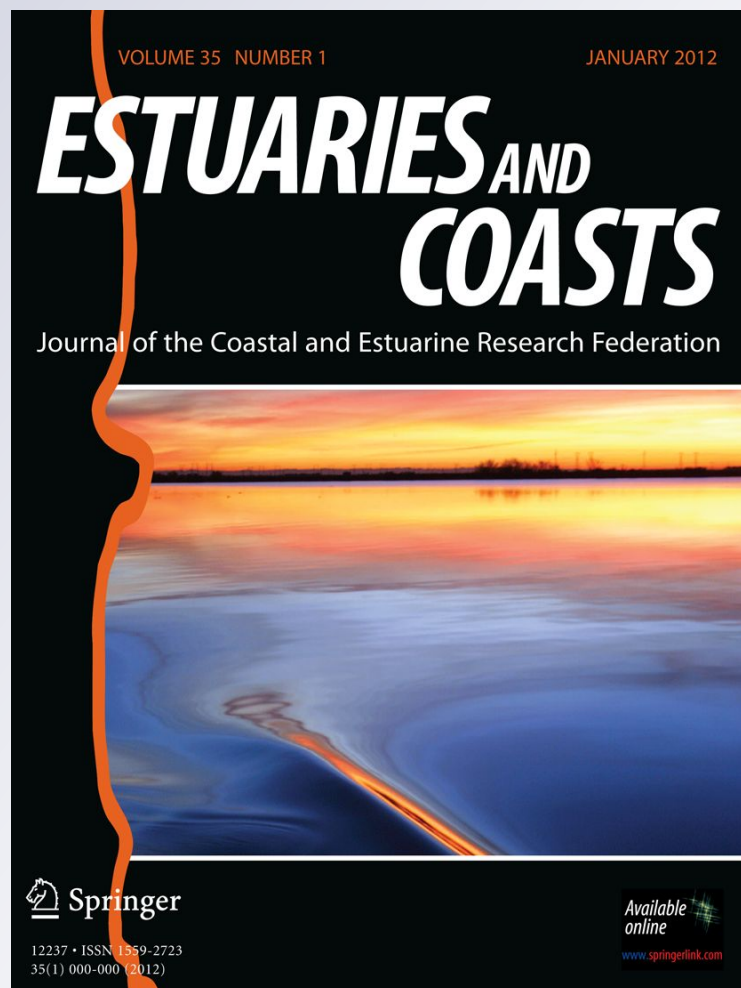
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Patterns of Surf Smelt, *Hypomesus pretiosus*, Intertidal Spawning Habitat Use in Puget Sound, Washington State

**Timothy Quinn · Kirk Krueger · Ken Pierce ·
Daniel Penttila · Kurt Perry · Tiffany Hicks ·
Dayv Lowry**

Abstract Surf smelt *Hypomesus pretiosus* are an important part of the Salish Sea food web and obligate beach spawners, yet little is known about the spatiotemporal distribution of spawning and beach characteristics related to spawning success. We counted smelt eggs at 51 sites around Camano Island, Puget Sound, Washington every 2 weeks for 1 year and at 13 of those 51 sites each month in the following year. At each site, we measured beach characteristics hypothesized to affect spawning habitat suitability as measured by egg abundance and mortality. Eggs were collected at 45 sites and pooled by month for analyses. Few sites ($N=10$, 19.6 %) contributed 87 % of total eggs and 89 % of all live eggs collected. Mean total egg counts at sites were higher ($p<0.019$) in Jul–Sep (1,790.7, SE=829.5) than in Jan–Mar (26.1, SE=10.2). Principal component and regression analyses suggested that aspect, fetch, solar radiation, and beach temperature predicted egg abundance but not mortality. Because a small proportion of sites appear to support most spawning activity, a conclusion consistent with year 2 egg counts, impacts to relatively few beaches could greatly affect surf smelt production.

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Introduction

Marine nearshore and intertidal environments are used for spawning and early rearing by diverse fishes (Moffatt and Thomson 1978; Carscadden et al. 1997; Nakashima and Taggart 2002) and invertebrates (Brousseau et al. 2004; Jackson et al. 2005). Intertidal spawning by fish occurs on coastlines of four continents and several species representing at least six families spawn on beaches, including silverside (Atherinopsidae), killifish (Fundulidae), puffer (Tetraodontidae), smelt (Osmeridae), righteye flounders (Pleuronectidae), and stickleback (Gasterosteidae) (Penttila 1995, 2007; Martin and Swiderski 2001). The nearshore environment of the Salish Sea (Puget Sound and Georgia Basin) is spawning and rearing habitat for several fish and wildlife species (Simenstad et al. 1979; Kozloff 1983; Kruckeberg 1991; Thuringer 2003; Townsend et al. 2006). At least three species of fish, surf smelt *Hypomesus pretiosus*, sand lance *Ammodytes hexapterus*, and rock sole *Lepidopsetta bilineata*, spawn in the intertidal zone of the Salish Sea (Schaefer 1936; Penttila 1995, 2007). Sand lance burrow into intertidal sediment during winter months (Quinn 1999), presumably as an energy conservation strategy (Winslade 1974), and Pacific herring *Clupea pallasii*, spawn on shallow subtidal macrophyton beds of the region (Gonyea et al. 1982; Penttila 1995). These species, commonly referred to as forage fish, are crucial components of marine food webs (Therriault et al. 2009) that are increasingly threatened by nearshore development from a growing human population (Penttila 2007; Anderson et al. 2009). Insufficient knowledge of the use of nearshore habitats by

forage fish limits our ability to guide development while conserving forage fish habitat.

Marine coastal areas, which comprise some of the most intensively developed landscapes throughout the world, are subjected to two frequent and important anthropogenic disturbances: shoreline armoring and removal of terrestrial vegetation (Fletcher et al. 1997; Griggs 2005; Dugan and Hubbard 2010; Krueger et al. 2010). Armoring to protect shorelines from erosion has a long history (Charlier et al. 2005), and armoring is expected to be more frequent and extensive because of rapid human populations growth near coasts (Crossett et al. 2004) and the perceived need to protect shorelines and developed areas from the effects of climate change (Scavia et al. 2002). Several recent studies in Puget Sound suggest that these disturbances can impair nearshore processes, including sediment delivery and transport and shading by riparian vegetation, which in turn affects species richness, abundance, and productivity (Romanuk and Levings 2006; Dethier and Berry 2010).

Better understanding of the spatiotemporal spawning patterns of forage fish will facilitate the conservation of their habitat as development along shorelines intensifies. We examine spatiotemporal patterns of surf smelt spawning because this species receives special protection from development, their behavior is relatively well understood, and conservation and research effort directed toward surf smelt might benefit other species. The obligate intertidal spawning behavior of surf smelt (hereafter smelt) in the Salish Sea is one of the best-documented aspects of their life history (Penttila 1995, 2007). Smelt spawn in the upper third of the tidal range in Puget Sound and appear to be tolerant of a wide range of salinities and wave energy regimes (Penttila 1978; 2001, 2002, 2007). However, recent research confirms that loss of nearshore vegetation reduces the suitability of smelt spawning habitat (Penttila 2001, 2002; Rice 2006; Rossell 2006; Lee and Levings 2007; Toft et al. 2007; Slack et al. 2010). We use suitability here to describe habitat quality, where quality can range from non-habitat to optimal habitat with maximal carrying capacity for a life stage (sensu USFWS 1981). Although smelt eggs appear to be somewhat resistant to thermal and desiccation stress, the eggs of fish spawning in summer and early fall suffer higher egg mortality on exposed beaches than on beaches with overhanging vegetation (Rice 2006; Lee and Levings 2007; Slack et al. 2010). In laboratory experiments, surf smelt eggs developed most successfully in a narrow relative humidity range (80–93 %) (Lee and Levings 2007) that on beaches is strongly dependent upon vegetative shading, sediment grain size (Penttila 2001, 2002), and both sediment and atmospheric temperature in the intertidal zone.

The effects of shoreline armoring on smelt spawning habitat is less clear, but shoreline armoring can decrease beach nourishment from eroding (feeder) bluffs and increase reflected wave energy, which lowers elevation and coarsens sediments of beaches in the upper intertidal zone (Baldwin and Lovvorn 1994; Toft et al. 2007). Spawning habitat in Puget Sound is typically found where waves and currents sort the available substrate into a sand–gravel mix with most sediment between 1 and 7 mm in diameter (Penttila 2001, 2002, 2007). Changes in the distribution of sediment to size ranges outside this window are expected to affect surf smelt spawning site selection and, perhaps, egg and larval mortality. In laboratory studies, small quantities of both suspended and settled silt were found to dramatically decrease larval smelt survival (Morgan and Levings 1989). On the other hand, Penttila (2007) suggested that most apparently suitable beaches in Puget Sound, based on substrate characteristics, do not support spawning activity, and population density, behavioral or environmental factors almost certainly also determine whether a beach supports spawning. As a result, in any given year, only approximately 30 % of the known smelt spawning beaches in Puget Sound support spawning (D. Penttila, unpublished data). While spawning seasons are coarsely known for some locations in Puget Sound; little is known about the temporal distribution of egg abundance or viability due to a lack of comprehensive temporal sampling.

The Washington Department of Fish and Wildlife (WDFW) protects fish life and habitat by administering the "Hydraulic Code" (Revised Code of Washington 77.55), which regulates work that uses, obstructs, diverts, or changes the natural flow or bed of state waters. The WDFW implements the law via the hydraulic project approval (HPA) permit process. Permits issued by the WDFW include provisions unique to the project type and physical setting that attempt to avoid, minimize, or mitigate for activities that may affect fish life in Washington's lakes, streams, rivers, and marine environments. Given our relatively rudimentary understanding of beach spawning fish ecology, provisions to protect forage fish are typically limited to work timing windows that determine when construction activities can occur. Further, all forage fish spawning sites as determined solely by presence of eggs are currently treated equally in the permitting process and in WDFW guidance to local governments.

Our objectives were to (1) characterize the annual spatiotemporal distribution of smelt spawning over a wide variety of physical conditions in a region of Puget Sound in an effort to improve the hydraulic permitting process and technical guidance to local governments involved in development and conservation planning; (2) investigate how variation in characteristics of the beach environment affect the suitability of spawning habitat, as measured by egg abundance and mortality rates; and (3) use statistical models to quantitatively explore relationships between habitat characteristics that we postulated might dictate the suitability of

smelt spawning habitat. Finally, we conducted an exploratory analysis of interannual correlations within and among sites and the consistency of spawn abundance across years.

Materials and Methods

Study Area

Camano Island is located in Puget Sound, Washington State, between Whidbey Island and the mainland (study area; Fig. 1) and is connected to the mainland by a bridge. It has an area of approximately 103 km² and a shoreline length of approximately 84 km based on the Washington Department of Natural Resources ShoreZone inventory data (http://128.208.23.127/website/DNR_Shorezone/DNR_SZ/szdoc/sz_hdr.htm), of which 31 % is armored (Puget Sound Nearshore Ecosystem Restoration Project 2009). We established 51 sampling sites along the shoreline of Camano Island (study area; Fig. 1) using a stratified random design. We selected study sites by calculating the total length of marine shoreline, excluding marshy wetland habitat along the northeast portion of the island. We excluded this habitat type because it has been consistently devoid of forage fish eggs in repeated sampling (D. Penttila, unpublished data) and because it has extensive low tide terraces composed of fine-grain sediments (silt) that are dangerous to traverse. We randomly established the first sampling site adjacent to the marsh in the first 300 m of the northeast end of the study area and, using ArcMAP (Version 9.3.1, ESRI, Redlands, CA, USA), located additional sampling sites clockwise at ~1.2 km intervals along the shoreline until we reached the northern end of the study area (Fig. 1). Sample site locations were transferred to Washington Department of Ecology oblique aerial photographs (http://apps.ecy.wa.gov/shorephotos/links.html) so that they could be located by boat using easily identifiable shore topographic features.

Sampling Approach

We visited all sampling sites by boat once every 2 weeks (referred to as a sample session) during each month beginning the week of 10 Sep 2007 and ending the week of 18 Aug 2008 (24 sample sessions). All sites were permanently assigned to one of three sampling routes. A two-person crew typically required 3 days to complete a sample session, with the crew sampling one route each day. We attempted to sample over consecutive days within a sample session, to space sample days between sessions as close to 12 days as possible, and to change route sampling order among sample sessions. The total number of sites sampled during a session and the sample schedule was based on logistical and ecological considerations. Sampling was performed on the
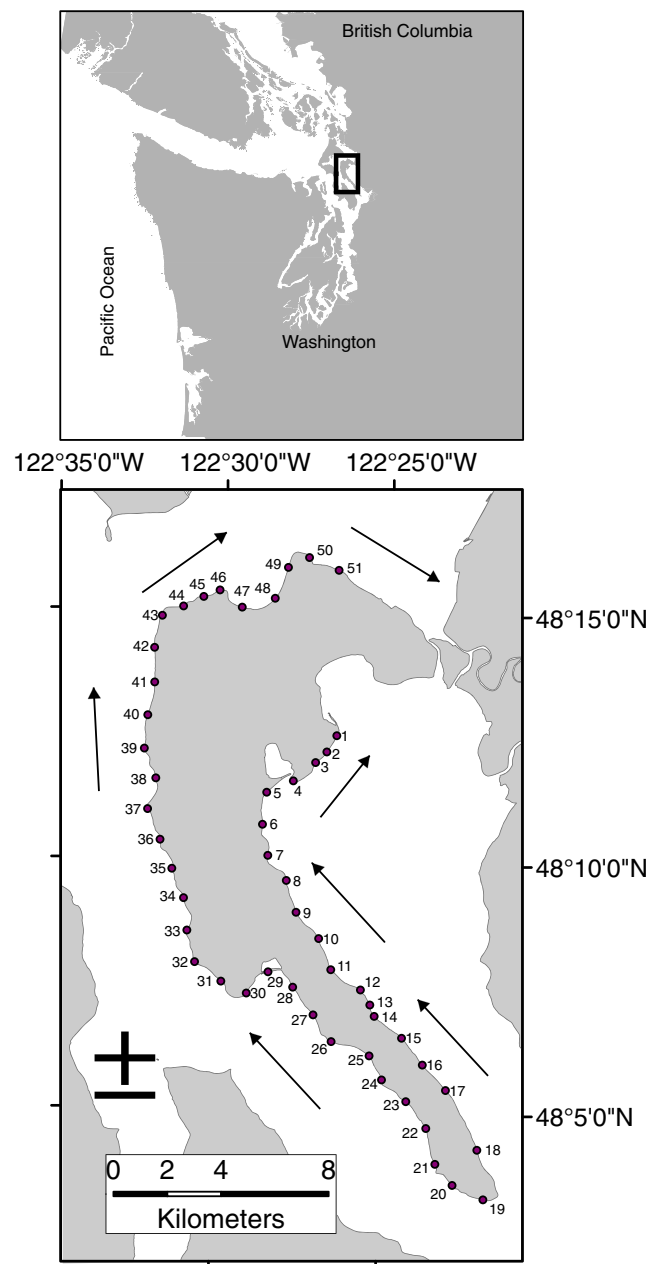

Fig. 1 Map of Camano Island, Puget Sound, Washington showing distribution of 51 sampling sites. **a** The geographic context of Puget Sound relative to the Pacific Ocean and British Columbia. **b** Camano Island with sampling sites labeled. *Arrows* indicate dominant sediment drift flow direction, not including small back eddies and interactions with shore features

lowest available daytime tides within each sample session. Given a two-person crew and the availability of suitable daytime tides, it was determined that the 51 sites could reliably be surveyed over the course of a year.

At each sampling site, we placed markers to establish two permanent, 30-m transects parallel to the waterline, one at +2.6±0.2 m and the other at +3.2±0.2 m above mean lower low water (MLLW). At each site, the permanent transect

elevation was determined by marking the water elevation at a specific time (during calm weather) for which tidal elevation was known. Hereafter, all beach elevations are in reference to MLLW and measured from the elevation of the two permanent transects.

Sampling for forage fish eggs consisted of taking a 500-ml scoops of surface sediment to a depth of approximately 5 cm at four locations (3, 11, 19, and 27 m) along each 30-m permanent transect (Moulton and Penttila 2001, 2006; Penttila 1995). Sediment and eggs from all subsamples for a given permanent transect were combined, transported to the laboratory, and processed on the day they were collected. Samples were processed by wet-screening them through a stacked series of sieves (4, 2, and 0.5 mm), progressively removing sediment while retaining eggs and egg-sized sediment. The remaining light fraction (fine sediment and eggs) was decanted into a washbasin, covered with 3 to 5 cm of water, and agitated to suspend lighter material, following Penttila (1995). After hydraulic winnowing, the surface 0.5–1 cm of the resulting deposit was skimmed off using a wide-mouthed sample jar. This winnowing process was repeated at least three times per sample to ensure adequate egg discovery probability (Moulton and Penttila 2001, 2006). The light fraction sub-sample was preserved in Stockard's Solution (aqueous mix of 4 % glacial acetic acid, 5 % formaldehyde, and 6 % glycerol). This preservative renders fish embryos opaque while leaving the yolk sac and other egg contents translucent, thus aiding in egg sample analyses. Using a dissecting microscope, eggs were identified to species, sorted into different cohort or age classes based on developmental stage, and scored as either live or dead (Penttila 1995). Live and dead eggs are treated as count data as opposed to density data since expanding them to the entire beach area would require egg distribution data that we did not collect and because we assumed that counts from standardized samples at each site were directly comparable. Our sampling method was developed based on over 30 years of sampling and analysis of more than 10,000 samples. Our previous work has shown that the collection of the top 5 cm of beach sediment collects virtually all smelt eggs and that collection, and processing of eggs on the same day as collection does not result in significant mortality.

In addition to the sampling described above, from August 2009 through July 2010, we sampled the upper permanent transect of 13 sites (sites 38–50, northwest portion of Camano Island) once per month. These sites were selected because, together, they exhibited a large range in annual egg counts during the first year of sampling. The intent of this additional sampling was to assess interannual correlations within and among sites and the consistency of high spawn abundance across years (i.e., 2007–2008 vs. 2009–2010).

Characterizing Sampling Sites

A suite of physical characteristics of all surveyed beaches were quantified once during the summer of 2009 to identify characteristics correlated with egg abundance and survival. Physical characteristics were selected based on a review of the literature describing intertidal spawning by fish and invertebrates and processes that affect the structure and function of beaches. Site-specific physical characteristics were measured in the field, whereas beach-scale physical characteristics were calculated using a geographic information system. Beach-scale physical characteristics were expected to change more slowly than, and affect the structure of, site-specific physical characteristics. We recognize that we did not measure some physical characteristics that may affect smelt spawning, but we expected to identify appropriate spatial scales and characteristics worthy of further study. At each sampling site, two temporary transects were established perpendicular to, and intersecting each end of, the 30-m permanent transect described above. Along these temporary transects, we measured beach slope between 1.3 and 3.2 m tidal elevation (Low_slope), between 3.2 m and mean higher high water (MHHW) (Mid_slope), and between MHHW and ordinary high water (OHW) (High_slope). The OHW was defined as that elevation where aquatic or semi-aquatic vegetation is replaced by terrestrial vegetation, or where terrestrial vegetation begins. At sites with no apparent physical evidence of the OHW (majority of sites), we estimated OWH to be MHHW +0.5 m. For each site, we then determined the (1) type of backshore control structure (berm, bulkhead, or bluff face); (2) elevation (Ele_control) of the toe of the bulkhead or bluff face, or in the case of a berm, the elevation of the slope break between the upper beach and berm; (3) elevation of the seaward (Ele_sea) and landward (Ele_land) edge of the drift wood zone; (4) width of the area where driftwood zone (Wood_width); and (5) volume of wood (Wood_vol) in the driftwood zone (i.e., 30 m × Wood_width). The driftwood zone was measured only where driftwood was present. Wood volume was determined during the summer of 2008 by tallying all wood pieces by 5-cm-diameter classes starting at a minimum of 10 cm at the thickest end and 60-cm-length classes starting at a minimum of 60 cm. Midpoints of diameter and length classes were used to calculate wood volumes at each site.

During the late summer period of high smelt egg abundance in 2008, additional sediment samples were collected along the upper transect at each site to evaluate beach sediment characteristics. Samples were spread out on shallow, plastic-lined trays and completely air dried in a protected alcove within a storage facility at the WDFW La Conner office. Drying typically took 3–7 days and was facilitated by gentle stirring and occasional transfer to a

sunny, undisturbed location. Dry samples were passed through a stacked series of sieves with mesh sizes of 0.1, 0.2, 0.4, 0.8, 1.7, 3.3, 6.7, 13.3, 26.7, and 53.9 mm. Material that passed through the 0.1-mm screen, which was invariably a tiny fraction of the substrate material, was retained in a shallow, solid pan. After weighing each fraction of the sample, we calculated D_{50}, which is the sediment size corresponding to 50 % of the cumulative frequency (the median), and the graphic standard deviation of D_{50} (D_{50}_SD) in Phi units, where Phi refers to particle size in terms of the mesh size at which a particular fraction was retained ($\Phi = -\log_2[\text{sieve mesh in mm}]$).

We estimated view to sky (Vis_sky) and global site factor (GSF) at each site using hemispherical photography [Nikon Coolpix 4500 digital camera and a 180° hemispherical lens (Delta-T Devices Ltd Model SLM4)]. GSF is defined as the proportion of global solar radiation, both direct and indirect, at a given site relative to an open, unshaded location and serves as an indicator of relative exposure among sites. Photographs were taken from the center of the upper transect during late summer (after vegetation leaf out and near the presumed peak of spawning) and processed using HemiView software (Version 2.1) (Rich et al. 1999). To minimize glare from the sun, photographs were taken during early morning or late afternoon and, whenever possible, on overcast days.

Temperature was recorded hourly from 30 July 2008 to 25 August 2008 at the midpoint of the upper transect at all sites using thermographs (Stowaway TidbiT data loggers, Onset Computer Corporation). The thermograph was attached to a 0.5-m piece of rebar with a cable tie and buried in the top 5 cm of the substrate. Thermographs were checked periodically to ensure their position in the top 5 cm of sediment where temperatures are relevant to developing eggs (Penttila 1995; Slack et al. 2010). We calculated two summary statistics from these data, mean daily maximum temperatures (Max_temp), and mean daily minimum temperatures (Min_temp) at each site.

At each sampling site, several beach-scale physical characteristics that could not be measured on the beach were derived from ShoreZone data (Shaffer et al. 2007). Beach sinuosity and concavity was quantified for each site. Beach sinuosity is the ratio of the shoreline length to the straight-line length (chord) between two points on the shoreline, equidistance from, and located on either side of, the site (Fig. 2). A sinuosity of 1 indicates a long straight section of beach whereas a value of 2 indicates that the shoreline length is twice the length of the chord connecting the two points. Concavity is the distance between the midpoint of the chord to the shoreline measured at a right angle to the chord (Fig. 2). Negative values indicate an exposed beach, and positive values indicate a protected beach. Sinuosity and concavity were calculated at 500 m (Concav_500, Sinu_500) and 5,000 m (Concav_5000, Sinu_5000). These

lengths were selected to help identify the spatial scales at which beach processes might affect spawning.

ShoreZone GIS data were also used to estimate beach aspect, which is defined as the normal angle (compass bearing) to the tangent line intersecting the sample site. Aspect serves as an indicator of solar exposure and has been identified as an important factor dictating the use of beaches for spawning by capelin *Mallotus villosus* (Nakashima and Taggart 2002). The distances from the site, along the aspect bearing, to the 10-m depth contour and to the nearest land were defined as Loc_10 and Fetch, respectively. A Short Loc_10 distance indicates a steeper nearshore slope, whereas a long length indicates a shallow slope. Aspect (in compass degrees) was converted to a standardized polar coordinate system, producing values ranging from −1 (south) to 1 (north), and redefined as Northness.

Statistical Analyses

Egg counts, including total eggs (Total_eggs), live eggs (Live_eggs), and dead eggs (Dead_eggs), were summarized by site, transect, and month to identify spatiotemporal spawning patterns and correlations with sample site characteristics. Counts were summarized by month rather than sample session because we were unable to sample all transects bi-monthly due to logistical issues (e.g., tide, inclement weather). For example, a monthly count at a site was obtained by averaging data from the bi-monthly sample sessions or by using single-visit counts where necessary for that month. Mortality rate, defined as Dead_eggs/Total_eggs, was calculated by month at each site but only when Total_eggs for that site month combination was ≥10 to avoid spurious estimates. Estimating counts and mortality rate by month allowed us to derive a relatively complete data set standardized by effort across months, sites, and transects. Count and mortality data were then summarized to: (1) mean monthly site data (mean$_{sites}$) calculated by summing data across all months at each site and dividing by the number of months sampled and (2) mean monthly data across all sites (mean$_{month}$), calculated by summing data across all sites each month and dividing by the number of sites sampled.

We used paired t tests to compare counts of Total_eggs (mean$_{sites}$) on upper versus lower transects and to compare mortality rates between upper and lower transects. Similarly, we used paired t tests to compare both counts (mean$_{sites}$) of Total_eggs and Live_eggs between summer July–September and winter January–March. We also calculated Pearson correlation coefficients to help understand the relationship between egg count metrics on lower versus upper transects. Only sites that had identical sampling effort (described above) were included in these comparisons. To determine if annual eggs counts per site in 2008–2009 were correlated with counts in 2009–2010, we calculated the Pearson correlation coefficient between counts of upper transect Total_eggs/site on sites 38–
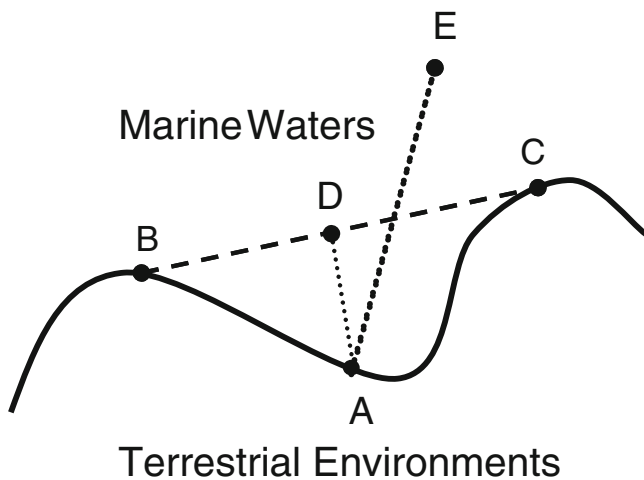
E

Marine Waters

C

D

B

A

Terrestrial Environments

Fig. 2 For each of the 51 beach sample sites (e.g., site *A*), we calculated a number of characteristics. Beach sinuosity is the ratio of the shoreline length (*BAC*) to the straight-line (*BC*) length between two points (*B* and *C*) on the shoreline, equidistance from, and located on either side of the sample site. Concavity is the distance from the midpoint of the chord to the shoreline (DA) measured at a right angle to the chord. Sinuosity and concavity were determined at two scales, 500 and 5,000 m. Concavity was negative when the sample site was exposed and positive when protected (shown here). Aspect was determined at the sample site (represented here by *AE*), and Loc_10 and Fetch were distances measured from the sample site in the direction of *AE* to the 10-m depth contour and nearest land, respectively

50 for 2008–2009 and 2009–2010. For all statistical tests, we chose $\alpha=0.05$ (Table 1).

Regression Analyses

We employed an information theoretic approach to explore the relationship between egg counts and physical characteristics of the shoreline. Following the methods described by Burnham and Anderson (2002) and based on extensive literature review and our field observations, we assembled eight candidate models a priori to explain variation in egg counts on the upper transect as a function of shoreline characteristics. We calculated Pearson correlations between egg count variables (i.e., Total_eggs, Live_eggs, and Dead_eggs) to determine the most appropriate response variables. We selected predictor variables and determined

Table 1 Pearson correlation coefficient matrix between variables describing surf smelt egg counts from 51 sites around Camano Island, Washington during 2007–2008

	Total_eggs	Live_eggs	Dead_eggs	Mort_rate
Total_eggs	1.000			
Live_eggs	0.972	1.000		
Dead_eggs	0.773	0.604	1.000	
Mort_rate	−0.289	−0.345	−0.049	1.000

the structure of the candidate models to allow comparison of predictor importance as measured at the spatial extent of sites and beaches. Before conducting the analyses, we examined the data to address regression assumptions (Beaudreau and Essington 2007). We removed beach characteristics for which we were missing relatively large amounts of data because this would reduce the sample size (number of sites) of the analysis. For pairs of predictor variables that were highly correlated ($r \geq 0.7$), we eliminated one and retained the characteristic deemed most interpretable. We then constructed a model containing the following characteristics, Northness, Fetch, Concav_5000, GSF, Max_temp, Wood_vol, and D_{50}, followed by construction of seven nested subset models using combinations of these characteristics (see Table 2). Before running regression models, we examined scatter plots of all individual shoreline characteristics (predictor) versus egg counts (potential response variable). When plots of residuals versus fitted values indicated a non-linear relationship, we attempted to linearize the relationship by systematically applying various transformations to the predictor variable until we maximized the r^2 of the simple regression. We used t tests to evaluate the null hypothesis that slope was equal to zero (Table 3).

The "best" models were based on corrected Akaike's information criterion (AIC$_c$), which indicates the best compromise between goodness-of-fit and model parsimony (Burnham and Anderson 2002). Models with delta AIC$_c$ less than 7 were regarded as supported by the data (Burnham and Anderson 2002, p. 70).

Principal Component Analysis

We conducted a principal component analysis (PCA) to condense the suite of beach characteristics measured/calculated in situ and from DNR ShoreZone data into a smaller set of compound components. We used PCA to help describe covariance patterns in beach characteristics for descriptive rather than confirmatory purposes (Tabachnick and Fidell 1989, p. 599). We hypothesized that beach characteristics were likely to respond to a few dominant environmental gradients, such as exposure to storm patterns, wave energy, and shoreform and that we could describe variation in beach characteristics in simpler ways by identifying these gradients.

Similar to the regression modeling above, we first removed variables describing beach characteristics for which we were missing relatively large amounts of data. For pairs of predictor variables that were highly correlated ($r \geq 0.7$), we eliminated one and retained only the variable deemed most interpretable. Although not strictly necessary for PCA, removing correlated variables increases the ratio of sample size to the number of observed variables. We examined univariate stem and leaf, box, and normality plots for each attribute to identify suspected outliers and, when they were

Table 2 Mean and range of response and predictor variables quantified in situ (site-specific) or derived from DNR ShoreZone data (beach scale)

Name	Scale	Description	Units	Mean	Range	r^2	p
Response variables							
Live_eggs		Mean live eggs per month	Eggs/month	3,967	0–93,374		
Dead_eggs		Mean dead eggs per month	Eggs/month	2,405	0–21,880		
Total_eggs		Mean total eggs per month	Eggs/month	6,372	0–113,643		
Predictor variables							
Vis_sky	Site	View to sky	Proportion	0.67	0.31–0.87	0.015	0.389
GSF	Site	Global site factor	Proportion	0.77	0.06–0.99	0.213	0.001
D_{50}	Site	Median sediment size	mm	6.4	0.6–30.3	0.068	0.067
D_{50}_SD	Site	Standard deviation of sediment size distribution	Phi	2.0	0.6–3.9	0.017	0.364
Low_slope	Site	Slope of lower beach	%	9.6	3.6–15.3	0.255	0.000
Mid_slope	Site	Slope of mid beach	%	13.7	3.3–132.0	0.074	0.054
Ele_control	Site	Elevation of the tidal control structure	m	3.7	2.6–4.4	0.058	0.089
Wood_width	Site	Width of the zone where drift wood collects	m	4.4	0.3–7.9	0.128	0.010
Wood_vol	Site	Volume of drift wood	m^3	6.0	0–77.3	0.012	0.442
Northness	Beach	Shoreline aspect: north (+1) to south (−1)	Index	−0.05	−0.96–0.99	0.574	0.000
Fetch	Beach	Distance to nearest land	m	6,218	1,692–14,446	0.120	0.013
Loc_10	Beach	Distance to depth of 10 m	m	1,303	66–10,599	0.034	0.194
Sinu_500	Beach	Sinuosity of 500 m segment	Index	1.0	1.0–1.6	0.022	0.320
Sinu_5000	Beach	Sinuosity of 5,000 m segment	Index	1.3	1.0–2.9	0.046	0.129
Concav_500	Beach	Concavity of 500 m segment	Index	−26.7	−430–229	0.007	0.569
Concav_5000	Beach	Concavity of 5,000 m segment	Index	−859	−4,615–3,463	0.000	0.995
Max_temp	Site	Mean of 27 max daily temps	°C	27.2	18.1–34.9	0.124	0.016
Min_temp	Site	Mean of 27 min daily temps	°C	18.6	15.5–21.5	0.233	0.001

We systematically applied various transformations to the predictor variable to meet normality assumptions and until we maximized the r^2 of the simple regression between that variable and log(Live_eggs + 1); p values were based on t tests to evaluate the null hypothesis that slope was equal to zero. Variables D_{50}, D_{50}_SD, Mid_slope, Ele_control, Fetch, Loc_10, and Min_temp were Log₁₀-transformed, and Northness and Max_temp were square root transformed. Wood_vol was transformed by (SQRT(Wood_vol) + SQRT(Wood_vol + 1))

not normally distributed, transformed variables to improve normality as determined by Lilliefors test (Systat 12). We conducted our PCA (Systat 12) using the correlation matrix of 20 beach characteristics (see Table 2 for list of variables) with no component rotation. To explore potential relationships among egg abundance and mortality rate, and principal components, we regressed log(Total_eggs +1) and mortality rate from the upper transect at each site against each of the most important principal components. We used data from the upper transect alone because these data were more complete, i.e., included a larger number of sample sites than the lower transect data set.

Results

Sampling was occasionally curtailed due to winter weather conditions, especially at a few sites. We completed sampling during 1,131 and 1,094 of 1,224 possible site visits (51 sites×24 visits) at the upper and lower transects,

respectively. When summarized by month, we sampled 607 and 592 of 612 possible site visits (51 sites×12 visits) at the upper and lower transects, respectively. By excluding December samples, we fully populated egg count data for all other site × month combinations for the upper transect. Likewise by excluding samples for December and for sites 14 and 44, we fully populated egg count data for all other site × month combinations for the lower transect.

Eggs were found at least once on 45 of 51 sites over the course of the study. The spatial distribution of egg counts around the island was clumped with about 20 % of sites contributing the vast majority of eggs (Fig. 3). Few sites (N=10, 19.6 %) contributed 87 and 89 % of Total_eggs and Live_eggs collected, respectively. Two relatively discrete areas of the shoreline, one on the eastern shore and another on the northwestern shore, had the highest egg abundance. Site 45 (Fig. 1) had the highest average eggs counts and over twice as many eggs as any other site. Annual counts of Total_eggs on upper transects (mean_sites=516.7, SE=225.4) were correlated (r=0.71, $t_{0.05(2),\ 47}$=6.856, p<0.001) with, but not

Table 3 Models considered in the information theoretic approach

Model	Variables	r^2	AIC_C	ΔAIC_C	$Exp(0.5 \times \Delta AIC_C)$	Rank
L1	Northness, Fetch, Concav_5000, GSF, Max_temp, Wood_vol, D_{50}	0.612	133.46	1.46	0.482	3
L2	Northness, Fetch, Concav_5000, GSF	0.611	138.47	6.47	0.039	7
L3	Northness, GSF, Max_temp	0.519	135.28	3.28	0.194	5
L4	Northness, Fetch, GSF, Max_temp, Wood_vol	0.596	133.10	1.10	0.578	2
L5	GSF, Max_temp, Wood_vol, D_{50}, Northness, Fetch, Concav_5000	0.612	133.46	1.46	0.482	3
L6	GSF, Max_temp, Wood_vol, Northness	0.561	133.98	1.98	0.371	4
L7	GSF, Wood_vol, Northness, Fetch, Concav_5000	0.632	138.44	6.44	0.040	6
L8	GSF, Max_temp, Northness, Fetch	0.580	132.00	N/A	N/A	1
M1	Northness, Fetch, Concav_5000, GSF, Max_temp, Wood_vol, D_{50}	0.024	51.69	2.95	0.229	4
M2	Northness, Fetch, Concav_5000, GSF	0.024	54.19	5.44	0.066	6
M3	Northness, GSF, Max_temp	0.011	48.74	N/A	N/A	1
M4	Northness, Fetch, GSF, Max_temp, Wood_vol	0.038	53.03	4.29	0.117	5
M5	GSF, Max_temp, Wood_vol, D_{50}, Northness, Fetch, Concav_5000	0.024	51.69	2.95	0.229	4
M6	GSF, Max_temp, Wood_vol, Northness	0.038	50.21	1.46	0.481	2
M7	GSF, Wood_vol, Northness, Fetch, Concav_5000	0.054	55.37	6.62	0.036	7
M8	GSF, Max_temp, Northness, Fetch	0.016	51.19	2.45	0.294	3

Models use either live egg (L1–8) or mortality rate (M1–8) as the response variable. AIC_C was used to determine the best model and other models in the subset were ranked for validity relative to the best model. For descriptions of variables and how they were transformed to improve normality, see Table 2

significantly different ($t_{0.05(2),\ df=48}=1.94$, $p<0.059$) from, annual counts of Total_eggs at lower transects (mean$_{sites}$= 125.6, SE=35.3). Egg counts varied seasonally, with peak abundance in late summer and early fall, though Live_eggs (albeit often in small number) were found during all months of the year at both transects (Fig. 4). Summer counts of Total_ eggs (mean$_{sites}$=1,790.7, SE=828.5) were significantly higher ($t_{0.05(2),\ df=48}=2.13$, $p<0.019$) than winter counts of Total_ eggs (mean$_{sites}$=26.1, SE=10.2), but summer counts of Live_eggs (mean$_{sites}$=955.8, SE=632.2) were not significantly different ($t_{0.05(2),\ df=48}=2.13$, $p<0.069$) from winter counts of Live_eggs (mean$_{sites}$=4.3, SE=1.7). Mortality rates peaked in summer at around 75 % just before egg counts reached their seasonal maximum and then declined to less than 20 % in late September at both transects (Fig. 4). Egg mortality rates on upper transects (mean$_{sites}$=0.589, SE=0.031) were significantly higher ($t_{0.05(2),\ df=33}=-3.21$, $p<0.003$) than mortality rates at lower transects (mean$_{sites}$=0.458, SE=0.031).

Egg counts at 13 sites were fairly consistent between years. Counts of Live_eggs on upper transects in 2009–10 were correlated ($r=0.756$, $t_{0.05(2),\ 11}=8.78$, $p<0.001$) with counts of Live_eggs in 2008–09 suggesting interannual stability in spawning site usage.

Regression Analyses

All potential response variables were correlated with each other, though some weakly (Table 1). Live_eggs and Total_ eggs were highly correlated ($r=0.972$), but r^2 values for

regression models were generally higher for Live_eggs; thus, we concentrated modeling efforts on Live_eggs and Dead_eggs as response variables.

Seven predictor variables (GSF, Low_slope, Wood_ width, Northness, Fetch, Max_temp, Min_temp) exhibited significant linear relationships with Live_eggs, with Northness having the highest r^2 (0.574). Nine predictor variables had significant linear relationships with Dead_eggs including the same seven variables as Live_egg regressions plus D_{50} and Sinu_5000. The best models for Live_eggs and Dead_eggs both contained GSF, Northness, and Max_temp (Tables 2 and 4). Additionally the best model for Live_eggs included Fetch. Concav_5000 and D_{50} were not included in the top models for either response variable or inclusion of Wood_vol varied (Tables 2 and 4).

Principal Component Analysis

We computed eigenvectors utilizing 16 beach characteristics and retained the first three principal components for interpretation (Table 5) based on the broken stick criterion (Jackson 1993). These first three components explained 23.83, 15.01, and 10.60 % of the total sample variance, respectively (Table 5). Based on the relative percent variance criterion alone, which suggests that the cumulative percent variance of the first one to three components should be greater than 70 %, this PCA does not dramatically reduce the dimensionality of the beach variation. Nevertheless, each of the first three components explains significantly

Fig. 3 Mean monthly egg counts (and mortality rates) calculated by summing egg counts (and mortality rates) across all months at each site and dividing by the number of months sampled. *Error bars* represent 1 standard error. **a** Upper transect, **b** lower transect. Note difference in scales of the first *y*-axis of **a** and **b**
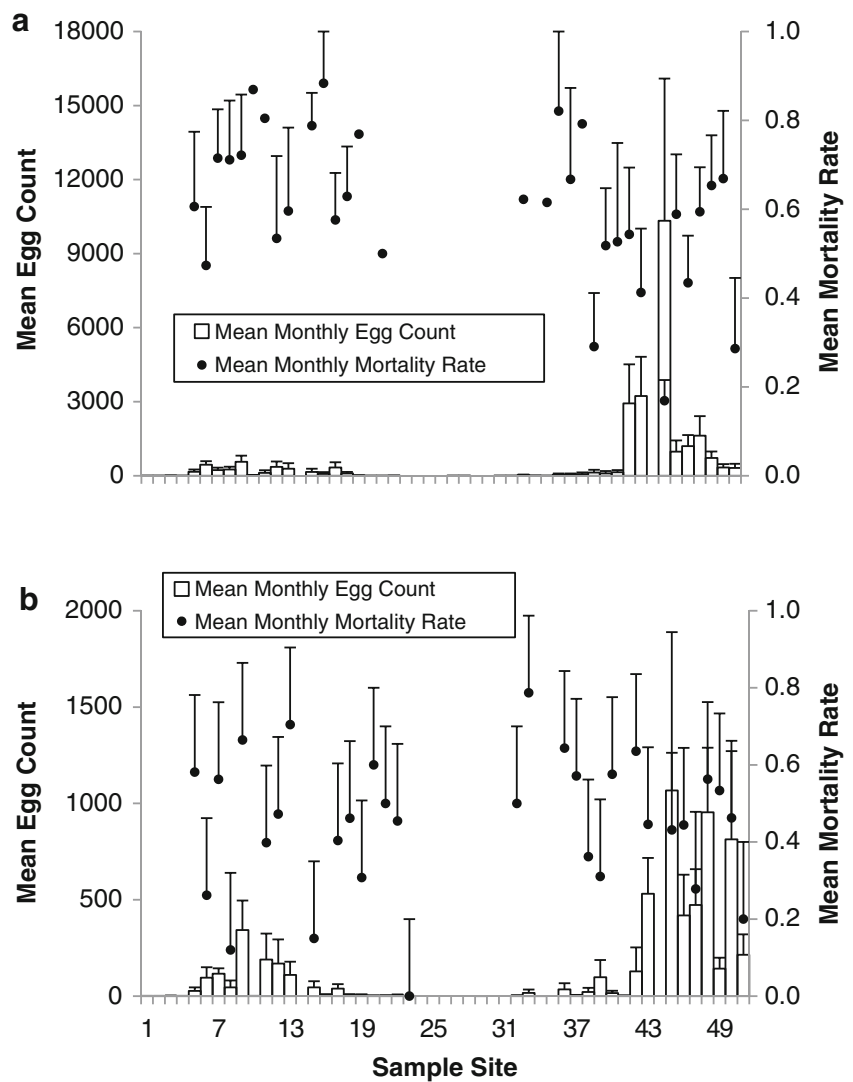
more variation than would be expected if there were no structure to the dataset. We based our interpretation of each component on variables with loadings > │0.45│ with more emphasis placed on higher loadings, particularly those > │0.60│ (Table 5).

The first component represents a gradient from south facing, relatively flat beaches with high GSFs, high elevation controls, large wood collection zones, large volumes of wood, and higher maximum sediment temperatures, to north facing, relatively steep beaches located in concave shoreforms with low GSFs and cooler maximum sediment temperatures. Note the strongly inverse relationship between Northness and GSF, as well as between Northness and Max_temp (Table 5). Beaches with southerly aspects would be expected to have higher sediment temperatures consistent with higher GSF. The second component represents a gradient of beaches within concave shoreforms, with large fetches, and large volumes of drift wood, to beaches in sinuous shoreforms, with small fetches, and small volumes

of wood. Three of the 16 original variables (Loc_10, Sinu_5000, and D_{50}_SD) did not load on either of the first two components and apparently do not contribute to the beach site gradient. Live_Egg counts were significantly associated ($F_{1,43}$=22.49, p<0.000) with PC1 scores (Log (Live_egg+1)=−8.50×PC1scores+2.20; r^2=0.34), but not PC2 scores (p=0.23).

Discussion

We found pronounced and consistent spatiotemporal patterns of surf smelt spawning on Camano Island, and these patterns can inform improved conservation efforts. The spatial distribution of egg occurrence was highly continuous, with smelt eggs found at nearly every site sampled over the course of a year, including many beaches where previous, less-intensive sampling failed to document smelt spawning. Although surveys to detect smelt spawning have been

Fig. 4 Mean monthly egg counts (and mortality rates) calculated by summing egg counts (and mortality rates) across all sites each month and dividing by the number of sites sampled. *Error bars* represent 1 standard error. **a** Upper transect, **b** lower transect. Note difference in scales of the first *y*-axis of **a** and **b**
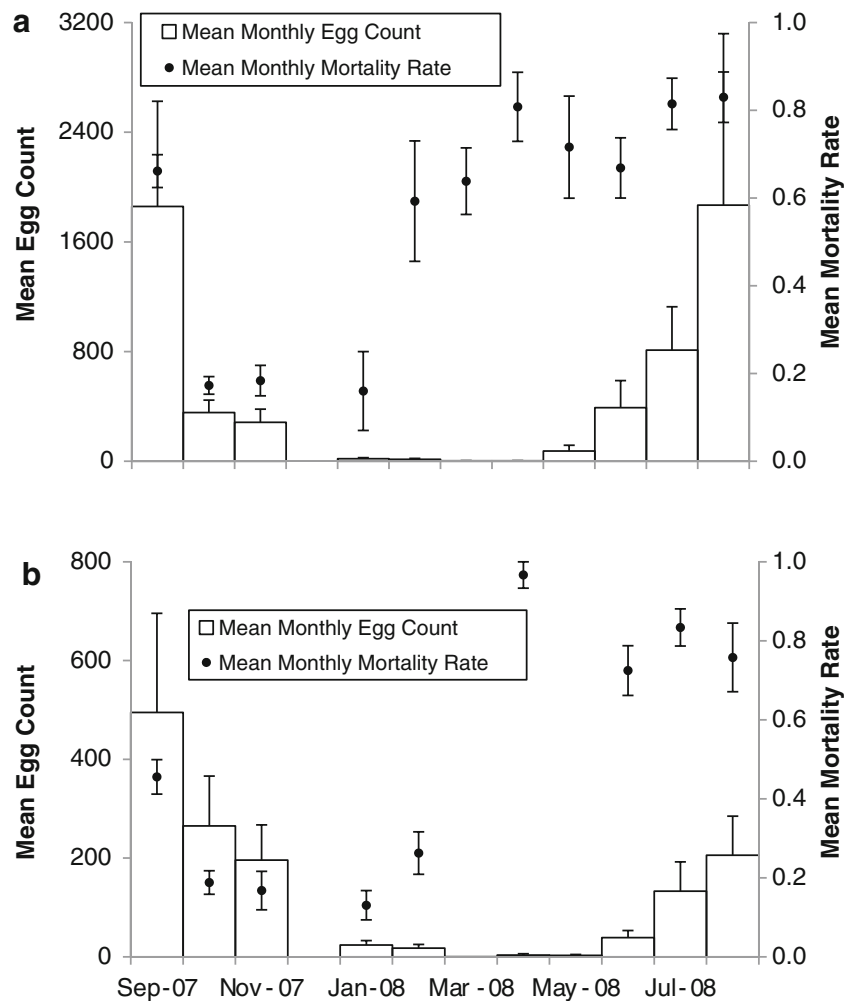
conducted throughout much of Puget Sound (Penttila 2007), our knowledge of spawning locations and their relative importance both intra- and inter-annually remains incomplete. Spawning beaches likely differ dramatically in production of smelt and their value for maintaining population abundance. The spatial distribution of egg abundance was nonuniform; sites on the northwestern edge of the study area (sites 42–48) contained up to several orders of magnitude more eggs than other regions of the island, a pattern that was consistent between years. This marked dominance in usage as spawning sites existed despite broad variation among these sites in some beach characteristics, including median sediment particle size, beach slope, backshore control type and height, wood band width, sinuosity, and concavity. However, in addition to being located in the northwest region of the study area, these sites were united by comparatively low maximum sediment temperatures, substantially greater fetch, narrow wood bands, and (except site 42) a north-facing beach aspect. The results of both our information theoretic approach and PCA support this overall trend toward high-use spawning beaches being characterized by

medium to high potential wave action (e.g., high fetch, narrow wood bands) and low solar exposure (e.g., north facing, low GSF, lower maximum temperature).

The results of our study are consistent with studies of capelin (*M. villosus*), suggesting that processes affecting spawning usage are likely similar among species and locations. Use of spawning beaches by capelin, as well as egg abundance on spawning beaches, has been linked to beach aspect (orientation) and the degree of substrate size sorting in Conception Bay, Newfoundland, Canada (Nakashima and Taggart 2002; Taggart and Nakashima 1987). The dominant orientation of high-use spawning beaches was northeasterly for capelin, which matches the geophysical context of spawning beaches in the current study with respect to fetch, prevailing wave action, and solar exposure. Additionally, Nakashima and Taggart (2002) noted that sediment size profiles within a beach may change seasonally as a consequence of changes in prevailing winds and resultant wave action. We only quantified sediment profiles during summer months so the degree to which those profiles change by season, and the resultant effects on egg retention and

Table 4 Standardized regression coefficients and p values for each independent variable describing beach characteristics used to explain live eggs counts (models L1–8) and mortality rate (models M1–8)

Effect	Model L1		Model L2		Model L3		Model L4		Model L5		Model L6		Model L7		Model L8	
	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p
Northness	0.619	0.000	0.564	0.000	0.635	0.000	0.606	0.000	0.619	0.000	0.695	0.000	0.629	0.000	0.549	0.000
Fetch	0.248	0.048	0.288	0.006			0.211	0.075	0.248	0.048			0.238	0.028	0.260	0.022
Concav_5000	−0.192	0.117	−0.133	0.184					−0.192	0.117			−0.164	0.104		
GSF	−0.205	0.098	−0.249	0.020	−0.187	0.121	−0.220	0.056	−0.205	0.098	−0.202	0.085	−0.256	0.016	−0.215	0.062
Max_temp	−0.018	0.878			0.008	0.944	0.039	0.733	−0.018	0.878	0.051	0.662			0.011	0.923
Wood_vol	0.144	0.240					0.143	0.223	0.144	0.240	0.215	0.062	0.168	0.122		
D_{50}	−0.032	0.785							−0.032	0.785						

Effect	Model M1		Model M2		Model M3		Model M4		Model M5		Model M6		Model M7		Model M8	
	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p	Coef	p
Northness	0.033	0.876	0.127	0.455	0.015	0.934	−0.025	0.900	0.033	0.876	−0.034	0.853	0.049	0.786	0.040	0.831
Fetch	−0.020	0.918	−0.122	0.449			−0.021	0.908	−0.020	0.918			−0.061	0.715	−0.077	0.646
Concav_5000	0.024	0.902	0.072	0.646					0.024	0.902			0.109	0.495		
GSF	0.074	0.700	0.042	0.797	0.067	0.695	0.080	0.642	0.074	0.700	0.079	0.644	0.051	0.758	0.075	0.664
Max_temp	−0.079	0.677			−0.090	0.595	−0.123	0.482	−0.079	0.677	−0.124	0.471			−0.090	0.596
Wood_vol	−0.094	0.623					−0.166	0.355	−0.094	0.623	−0.173	0.300	−0.200	0.246		
D_{50}	−0.089	0.636							−0.089	0.636						

For descriptions of variables and how they were transformed to improve normality, see Table 2

Table 5 Component loadings for six principle components derived from analysis of beach attributes measured on 46 beaches around Camano Island in Puget Sound

Beach attribute	PC1	PC2	PC3	PC4	PC5	PC6
Northness	**−0.770**					
Max_temp	**0.654**					
GSF	**0.625**					
Ele_control	0.577	0.462				
Min_temp	0.577					
High_slope	−0.574					
Mid_slope	−0.499		0.489			
Concav_500	−0.453	0.469				−0.475
Concav_5000		**0.615**				
Fetch		0.591				
Wood_vol		0.580				
Sinu_500		−0.542				
D_{50}		−0.468				
Loc_10			**0.714**			
Sinu_5000			0.485	−0.541		
D_{50}_SD					−0.573	−0.464

Loadings with absolute values < │0.45│ were considered unimportant (Tabachnick and Fidell 1989) and not included here. Loadings > │0.60│ are shown in bold for emphasis. For descriptions of variables and how they were transformed to improve normality, see Table 2

viability, cannot be directly evaluated. In addition, other factors such as predation on and off the beach and larval transport and rearing undoubtedly contribute to the suitability of surf smelt spawning sites. These factors were beyond the scope of our work but clearly warrant further study.

We postulate that the suitability of a beach for spawning by smelt is due primarily to characteristics of the beach and adjacent beaches. Beach characteristics are in turn determined by sediment source, exposure, and the energy available to shape beach morphology. Wave action influences beach form through erosion, transport, and deposition of sediment and organic matter (Dugan and Hubbard 2006, 2010; Patsch and Griggs 2006). Puget Sound is populated by numerous feeder bluffs composed of glacial till that contribute sediment to beaches. Due to limitations in fetch and the predominant direction of storms relative to the north south orientation of shorelines, wave action is typically oblique to shore in Puget Sound (Finlayson 2006; Johannessen and MacLennan 2007; Shipman 2008, 2010). This geomorphic setting produces sediment drift cells along which wave action and sediment turnover are relatively stable and predictable, barring storm events and human disturbance of the shoreline. The suitability of beaches for smelt spawning is likely related to its position within a drift cell. We suggest that on beaches where wave action has sorted the sediment appropriately, water percolation and retention may be balanced such that smelt eggs in the upper intertidal remain damp but not continually immersed. Moderation of relative humidity in a narrow window (80–93 %) is critical to surf smelt egg development (Lee and Levings 2007). As the prevailing winds in Puget Sound are strong and come from the southwest in winter and weaker and

northerly in summer (Overland and Walter Jr. 1983; Finlayson 2006), it is possible that beaches on southern Camano Island have, over geologic time, developed into suboptimal smelt spawning habitat through wave action (but see comments on seasonal beach reconditioning above). This is borne out in the nearly complete lack of eggs in sites 23–32 along southwest Camano Island and the prevalence of finer sediments along these beaches as compared to the high-use beaches (D_{50}=6.73 vs. 4.70). However, the small number of drift cells identified on Camano Island precludes meaningful statistical analysis.

The suitability of a beach for spawning by smelt is also related to its exposure to incident solar radiation, which is the greatest on south-facing beaches. As a consequence of exposure, the average temperature of intertidal sediments on south-facing beaches can, all other characteristics being equal, be expected to be higher than on north-facing beaches. Recent studies have shown that smelt egg mortality increases with increasing exposure to solar radiation, sediment temperature, and desiccation (Penttila 2001, 2002; Rice 2006; Rossell 2006; Lee and Levings 2007). These findings are consistent with the pattern of smelt egg abundance across the gradient represented by PC1. Two other lines of evidence in our data suggest that high summer temperatures and associated effects (e.g., low humidity) may be related to poorer spawning habitat suitability. First, smelt eggs at lower elevation transects generally had lower mortality rates than eggs at higher transects, although egg abundance was also lower. This suggests that thermal and desiccation stress were both minimized lower on the beach. Furthermore, egg mortality declined markedly after August at both upper and lower egg transects with the seasonal decrease in atmospheric temperature and the return of

regular precipitation. The preferred tidal height for placement of eggs at a given spawning site is likely a tradeoff between thermal and desiccation stresses at higher intertidal elevations and increased relative humidity and predation stresses at lower elevations.

Beaches are commonly armored with concrete or rock revetments to prevent erosion or to gentrify yards (Kraus and McDougal 1996; Holsman and Willig 2007; Shipman 2010). When revetments are placed within the marine intertidal zone, they can have cascading effects resulting in changes to the beach profile, coarsening of beach sediments, loss of large woody debris, and increased wave energy to the foreshore (Holsman and Willig 2007; Dethier and Berry 2010; Dugan and Hubbard 2010). Humans can also increase exposure to solar radiation of the beach as a result of clearing the land of vegetation for construction and to provide an unobstructed view of the water. The direct detrimental effects on gross habitat characteristics and microclimate, exacerbated by sea level rise as a consequence of climate change (Krueger et al. 2010), indicate that shoreline armoring and marine riparian zone elimination represent two important threats to the continued reproductive capacity of surf smelt in Puget Sound (Penttila 2007; Rice 2010).

Management Implications

The challenge of conservation is finding ways to minimize the loss of biodiversity with limited financial and human resources (Bottrill et al. 2009). Thus, natural resource managers are commonly confronted with three fundamental questions: (1) what needs protection, (2) where should it be protected, and (3) how should it be protected (Primack 2010, p. 351). While substantial scientific uncertainty remains regarding the characterization of suitability of surf smelt spawning habitat and the processes that create and maintain them, our results along with other important work on beach ecology cited herein suggest a number of immediate actions that could improve conservation of surf smelt spawning habitat. First, given the high demand for additional shoreline development and the fact that nearly 30 % of Puget Sound marine shoreline and 31 % of Camano Island is currently armored (Puget Sound Nearshore Ecosystem Restoration Project 2009), the most important spawning beaches should be identified and afforded more protection and restoration effort. That is, beaches in northwest Camano Island and those with low summer temperature, north-facing aspect, and relative large fetch are more important for smelt spawning than other beaches and thus should receive additional consideration during the HPA and other shoreline construction permitting processes. In addition, the drift cells in which these beaches occur should also be considered as important conservation targets, particularly in terms of maintaining sediment delivery and transport processes.

Where development will occur, armoring should be permitted only where it is critically necessary to protect capital investments and then placed above the ordinary high water mark based on future sea level rise predictions. All shoreline vegetation should be maintained, especially trees that shade the intertidal region of the beach. While spawning sites with northerly aspects may currently be more resilient to high temperatures than sites with southerly aspects, increasing sea and air temperatures associated with climate change may diminish the suitability of all beach sites.

Finally, while the value of providing best available science is clear in cases involving imminent and permanent change, such as human development of the nearshore, we also urge commitment to better use of scientific information especially where we have learned from past mistakes. For example, the importance of spawning during seasons with low egg abundance should not be discounted. Although total smelt egg abundance and the number of live eggs were the highest in summer, eggs were often found in abundance during winter when mortality was relatively low; suggesting that smelt that spawn in winter might substantially contribute to the population, at least during years or at locations when summer mortality is especially high. Conserving sufficient habitat quantity and suitability for expression of such variations in life history might facilitate species persistence in highly variable environments (Caswell 1983), or serve as locations of bet-hedging (Helfman et al. 1997), that ensure the long term survival of smelt faced with disturbance. These conservation actions might be especially important as environments become more variable due to human actions and climate change (Reed et al. 2010).

We have two concluding thoughts relative to information needs. First, given the high demand for additional shoreline development, there is a tremendous need to better understand how typical shoreline development affects beaches as smelt spawning habitat both at the site and larger (e.g., drift cell) scales. Second, although widespread surveys to detect smelt spawning have been completed throughout much of Puget Sound (Penttila 2007), our knowledge of spawning locations and their relative importance both intra- and inter-annually remains incomplete over much of Puget Sound. Failure to detect eggs in a few samples remains poor evidence of absence of smelt spawning just as relatively low abundance of eggs in a few samples at a site may not be indicative of the importance of that site over an annual cycle. We encourage a more thoughtful approach to permitting new shoreline armoring projects in Puget Sound given existing survey data. Specifically, projects with potential to affect site or drift cell characteristics should receive forage fish spawning surveys for at least 1 year similar to the surveys we conducted on Camano Island. Data from these surveys would increase the probability of avoiding false negative results and begin to test the applicability of the

Camano Island spawning suitability model outside of our study area.

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