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Effects of Shoreline Modification on a Northern Puget Sound Beach: Microclimate and Embryo Mortality in Surf Smelt (*Hypomesus pretiosus*)

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ABSTRACT: Human alteration of Puget Sound shorelines is extensive yet its ecological consequences are largely undocumented. This study evaluates differences between natural and heavily modified beaches in terms of microclimate and one aspect of biological condition. Electronic data loggers were placed at a tidal height of approximately 3.7 m (12 ft) above mean lower low water during July 16–20, 2001, to monitor light intensity, substrate and air temperatures, and humidity. Substrate samples were collected at the end of the monitoring period to evaluate condition and density of eggs from surf smelt (*Hypomesus pretiosus*), a forage fish species that spawns on gravel-sand beaches in the upper intertidal zone. The modified beach had significantly higher daily mean light intensity, air temperature, and substrate temperature, and significantly lower daily mean relative humidity. Particularly striking were the differences in substrate temperature, which, on the natural beach, ranged from 12.1°C to 18.2°C (mean = 14.1°C) and on the modified beach ranged from 14.4°C to 29.4°C (mean = 18.8°C). In addition to these different means and more extreme values, microclimate conditions on the modified beach were more variable, indicative of a less buffered environment. The proportion of smelt eggs containing live embryos on the altered beach was approximately half that of the natural beach.

Introduction

The nearshore ecosystems of Puget Sound are crucial in the life cycle of many fish and wildlife species (Simenstad et al. 1979; Kozloff 1983; Simenstad 1983; Phillips 1984; Kruckeberg 1991). They also are subjected to many human influences, including shoreline armoring and removal of terrestrial vegetation, two of the most prevalent and severe anthropogenic disturbances in the region (Williams and Thom 2001; PSWQAT 2002). While little is known about the ecological consequences of anthropogenic shoreline modification in Puget Sound, available studies suggest impairment (Thom and Shreffler 1994; Levings and Jamieson 2001; Penttila 2001; Romanuk and Levings 2003; Sobocinski 2003). This study examines effects of shoreline modification on beach microclimate (light, air and substrate temperature, and humidity) and one aspect of biological condition (embryo mortality in an intertidally spawning fish). It also considers the implications of shoreline alteration on the overall ecology of nearshore Puget Sound, including cumulative effects at the landscape level.

Generally, nearshore environments include the region between the lower extent of light penetration on the seaward side of the shoreline and the extent of direct interaction in the form of sediment supply from adjacent bluffs or shading and bank stabilization by terrestrial vegetation (Williams and Thom 2001); that is the sublittoral photic, littoral, and supralittoral zones combined. As an ecotone between terrestrial and aquatic estuarine ecosystems, the nearshore performs a number of distinctive ecological functions including the generation, accumulation, and decomposition of detritus that can be an important part of the estuarine and terrestrial food webs (Day et al. 1989; Polis and Hurd 1996; Colombini and Chelazzi 2003; Dugan et al. 2003) and as foraging, spawning, rearing, and migration habitats for a rich variety of organisms (Day et al. 1989; Brennan and Culverwell 2004). Many of these species are recreationally and commercially important. In Puget Sound these include five species of Pacific salmon (*Oncorhynchus* spp.) and four species of anadromous trout (*Oncorhynchus* spp. and *Salvelinus* spp.) comprising many distinct population segments, three of which (Puget Sound Chinook salmon [*O. tshawytscha*], Hood Canal summer chum salmon [*O. keta*], and bull trout [*S. confluentus*]), are listed as threatened under the Endangered Species Act (Johnson et al.

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1997; Myers et al. 1998; USFWS 1999). Another salmonid (Puget Sound coho [*O. kisutch*]) is proposed for listing (Weitkamp et al. 1995).

Puget Sound shorelines have experienced major impacts as the result of human activity, including diking, filling, armoring, and devegetation for purposes of agricultural, industrial, and residential development. At least one third of the linear shoreline has been modified by humans (PSWQAT 2002). Physical effects of these activities (hardening and deepening of the shoreline, loss of structural complexity, and loss of connectivity between aquatic and terrestrial environments) occur immediately and can persist for decades (Macdonald et al. 1994; Williams and Thom 2001). Long-term effects are largely the result of changes in sediment dynamics and the reduction or elimination of the supply of organic matter from the adjacent terrestrial environment. The substrate can coarsen, the beach slope steepen, and the structural complexity and organic debris accumulation decline (Macdonald et al. 1994; Williams and Thom 2001).

Because physical shoreline conditions are a primary influence on biological processes (Ricketts et al. 1985; Day et al. 1989; Ricklefs and Miller 2000; Knox 2001), extensive physical modifications can potentially affect species composition, abundance, and distribution; the flow of nutrients and organic matter; and many other factors. Anthropogenic alterations of freshwater riparian ecosystems have such effects (Kelsey and West 1998; Naiman et al. 1998). While little empirical evidence exists on the ecological consequences of shoreline modification in Puget Sound, available information suggests significant adverse effects can occur, including loss or degradation of spawning substrate and food resources for fishes (Thom and Shreffler 1994; Levings and Jamieson 2001; Penttila 2001; Brennan and Culverwell 2004). One specific example is the reduction in taxonomic richness and abundance of invertebrate assemblages on armored beaches when compared to natural beaches (Romanuk and Levings 2003; Sobocinski 2003). Such effects are likely to be partially due to changes in microclimate, the local suite of climatic conditions near the ground (Geiger 1965; Brosofske et al. 1997; Chen et al. 1999). Drastic changes in light, thermal, and moisture conditions can have severe biological consequences (Ricklefs and Miller 2000). On estuarine shorelines, removal of overhanging supralittoral vegetation increases beach exposure to sunlight, increasing temperature and evaporation and drying out beach environments. Reductions in structural complexity and accumulation of organic debris on altered beaches may reduce capacity for water retention, further contributing to drying. Given the sensitivity of intertidal organisms (Pugh and Macalister 1994; Rafaelli and Hawkins 1996) and geochemical processes (Valiela 1995) to drivers such as temperature and moisture conditions (Jedrzejczak 2002), microclimatic changes from physical disturbance at the shoreline could influence the distribution and behavior of organisms and the flux of energy and material in the nearshore. These and other potential effects of anthropogenic changes in estuarine and coastal marine shoreline microclimate are poorly documented.

Shoreline Modification and Surf Smelt Spawning

One major concern regarding shoreline modification is adverse effects on essential nearshore fish habitats. Intertidal beaches provide spawning habitats for a number of fish species (DeMartini 1999; Martin and Swiderski 2001). Potential benefits of intertidal spawning include refuge of embryos from aquatic predators and increased oxygenation and rate of development of embryos while not immersed by the tide. Potential risks of intertidal spawning include time and energy expended during tidal migration of spawning adults, exposure of spawning adults and embryos to terrestrial and avian predators, and physiological stress of embryos while not immersed. Embryos of intertidal spawning fishes often have broad thermal tolerances and plasticity in incubation duration that allow them to persist in the variable and harsh intertidal environment (DeMartini 1999; Smyder and Martin 2002), but environmental extremes can be hazardous to developing embryos. Some upper intertidal spawning species protect embryos from thermal and desiccation stress by burial in the substrate or deposition in beach debris or abandoned burrows of other organisms (Middaugh et al. 1983). Intertidally spawning fishes in Puget Sound also may, to some degree, depend on shade and debris in the upper intertidal to protect their incubating embryos. Anthropogenic changes in shoreline microclimate will change the intertidal incubating environment, potentially altering developmental rates or increasing physiological stress in fish embryos.

In Puget Sound, most concern in this regard is focused on the surf smelt (*Hypomesus pretiosus*), a recreationally important pelagic fish that is a common food item for many fish and wildlife species. Surf smelt occur throughout Puget Sound and spawn on upper intertidal, gravel-sand beaches (Schaefer 1936; Thompson et al. 1936; Loosanoff 1937). Except for Pacific sand lance (*Ammodytes hexapterus*), which also spawn on upper intertidal beaches but only during winter months, surf smelt are unique among Puget Sound fishes in their obligate spawning use of these habitats. Surf smelt spawn at various times of year, but in much of

northern Puget Sound, summer is the peak spawning season (Loosanoff 1937; Penttila 1973, 1978, 1995). Spawning typically occurs on extreme high tides during evening or night. At spawning, eggs adhere to substrate particles and incubate for approximately 10 to 21 d before hatching when immersed and agitated by tidal inundation.

Temperature and moisture conditions of the substrate influence the survival and rate of development in surf smelt and other intertidal spawners (Yap-Chiongco 1941; Frank and Leggett 1981a; DeMartini 1999; Smyder and Martin 2002; Lee personal communication). Because of warmer weather and higher light levels during the summer months, it has been postulated that smelt embryos incubating on intertidal beaches in summer would be most exposed to excessive thermal stress and desiccation, especially at armored spawning beaches that have no terrestrial vegetation (Schaefer 1936; Penttila 1973). Historical data from Puget Sound summer beach spawn surveys showed that beaches without terrestrial shoreline vegetation had significantly lower proportions of live smelt embryos (Penttila 2001, Fig. 1). Thermal stress and desiccation were proposed by Penttila (2001) as the causes of lower embryo survival on the unvegetated beaches; but no detailed assessment of the physical environment was made nor was anthropogenic alteration of beaches an explicit factor in the analysis.

To evaluate the potential effects of shoreline modification on summer shoreline microclimate and surf smelt embryo survival, I compare an armored beach with no terrestrial shoreline vegetation to an unarmored, naturally vegetated beach. I tested two specific null hypotheses: there would not be significant differences between the natural and modified beaches during periods of sunny summer weather in terms of light intensity, substrate temperature, air temperature, and relative humidity; and surf smelt egg density and proportion of eggs containing live surf smelt embryos would not be significantly lower on the modified beach.

Materials and Methods

Study Sites

The two adjacent beaches used in this study are located at the northern end of Camano Island, Washington (48°15.1′N, 122°30.5′W), a known area of summer surf smelt spawning (Loosanoff 1937; Penttila 1995). Similar to much of Puget Sound, the shoreline in the study area consists primarily of unconsolidated glacial material with mixed gravel-sand beaches and upland banks that, under natural conditions, are often forested with a mix of conifers and deciduous hardwoods, depending on the slope

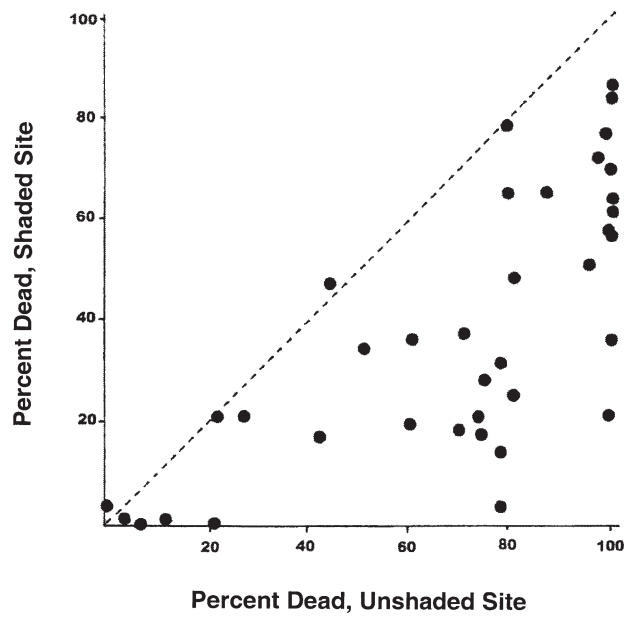

Fig. 1. Scatter diagram of surf smelt embryo mortality at 37 sets of paired shaded and unshaded beaches. From Penttila (2001); reprinted with permission.

and exposure (Downing 1983; Kruckeberg 1991). One beach has no overhanging terrestrial vegetation and is armored with a vertical concrete bulkhead at approximately +4 m relative to mean lower low water (MLLW). The adjacent beach is not armored and has extensive terrestrial vegetation dominated by mature big leaf maples (*Acer macrophyllum*). Study sites were monitored during July 16–20, 2001, the early or middle part of the spawning season (Loosanoff 1937) and a period of sunny but not exceptionally hot weather for summer in the region.

Data Collection

At one location in the middle of each beach at a tidal elevation of approximately +3.7 m MLLW, electronic data loggers were installed at the start of the 5-d monitoring period. Combination temperature and relative humidity loggers (Onset HOBO model H08-032-08) enclosed in radiation shields (Onset model RSI) were mounted 1 m above the ground on 1.9-cm galvanized pipes hammered into the substrate. Light intensity loggers (Onset HOBO model HLI) enclosed in plastic petri dishes were glued to the tops of the radiation shields, and digital temperature loggers (Onset HOBO model H01-001-01) in white, waterproof cases were pressed into the substrate and tied to the base of the mounting poles so that they were flush with the substrate surface. All data were recorded at 5-min intervals. After 5 d all loggers were removed from

the beaches, and the data downloaded and separated into day (sunrise to sunset) or night (sunset to sunrise) groups. Due to incomplete data collection on the first day, only four complete sets of data from day and night periods were analyzed.

At the end of the study period, five surficial (top 3 cm) substrate samples were collected at the same tidal elevation as the loggers. Glass 4-oz jars were used to scoop bulk substrate samples at approximately 2-m intervals along a transect parallel to the shoreline and centered on the logger locations. These samples were preserved in Stockard's solution (5% formaldehyde and 4% acetic acid). One subsample (0.5-cm deep layer of sediment in 8-cm diameter Petri dish) from each replicate substrate sample was then examined under a dissecting microscope for counts of total, live, and dead smelt eggs. Eggs were considered dead if they were opaque, obviously desiccated, broken open, or no intact embryo was visible in the egg.

Data Analysis

Statistical analyses consisted of pairwise (by day), two-tailed *t*-tests on daily minimum, maximum, and averages of the environmental variables, and unpaired, one-tailed *t*-tests on smelt egg data. One-tailed tests on the egg data were justified based on the results of Penttila (2001), that showed a significantly lower proportion of live versus dead embryos on unshaded beaches. To reduce the effects of nonnormal data distribution and heteroscedasticity, egg count data (eggs cm^{-3}) were transformed using the log (x + 1) transformation, and proportion live data were transformed using an arcsine square root transformation (Zar 1996). Significance criterion was set at $\alpha \leq 0.05$.

Results

Three of the four physical variables measured (substrate temperature, air temperature, and relative humidity) were different between the two beaches for nearly the entire study period, even at night (Fig. 2). The obvious exception was light intensity, which was higher on the altered beach during the day but showed no difference between the two beaches at night due to the absence of sunlight. The observed differences suggest that enough heat was absorbed by the altered beach during the day to maintain higher substrate and air temperatures through the night. It is impossible to know to what extent the lower humidity on the altered beach is the result of these higher temperatures or the lack of vegetation but it is probably a combination of both. Daily mean values for all four physical variables were significantly different ($p \leq 0.007$; Table 1). The altered beach had signifi-

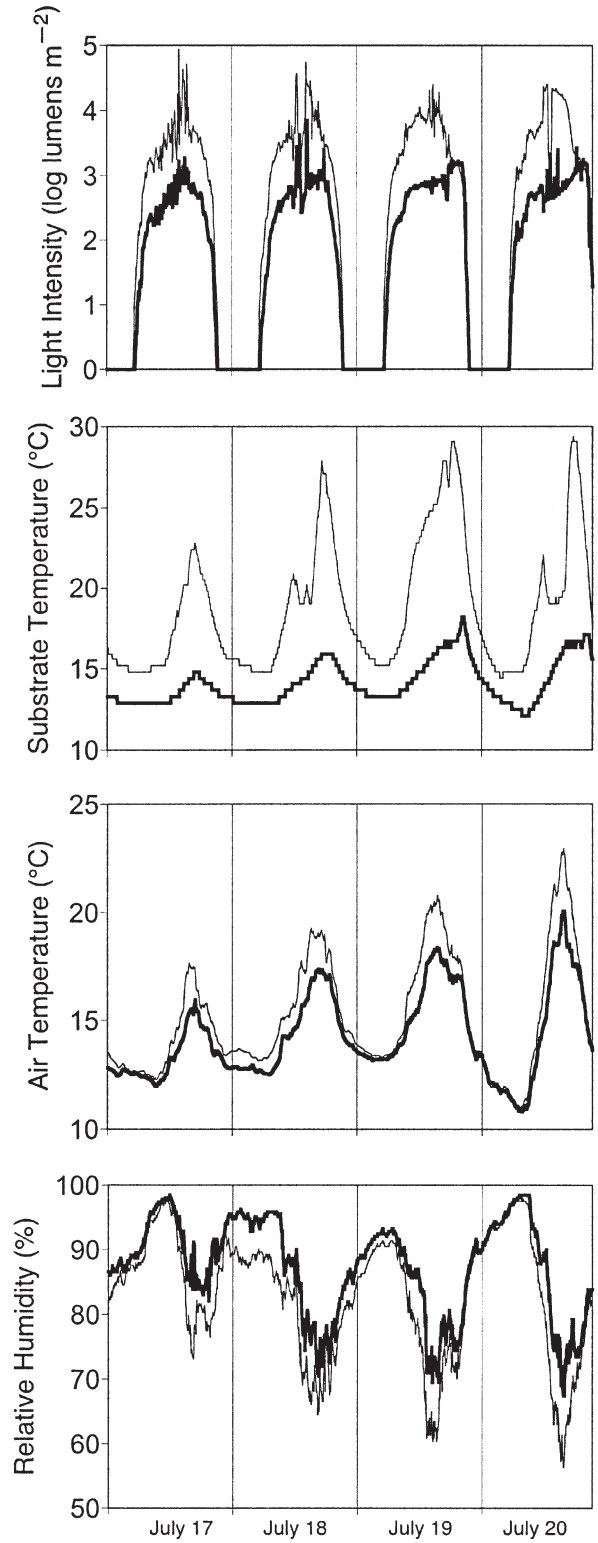

Fig. 2. Light intensity, substrate temperature, air temperature, and relative humidity at the natural (thick line) and modified (thin line) beaches over four sunny days in July 2001.

TABLE 1. Average (± SD) daily minimum, maximum, and mean values for physical measurements over 4 d at the natural and modified beaches. Asterisk indicates significant difference between the natural and modified beaches at $p \leq 0.007$ ($n = 4$).

	Light intensity (log lumens m^{-2})		Substrate temperature (°C)		Air temperature (°C)		Relative humidity (%)	
	Natural	Modified	Natural	Modified	Natural	Modified	Natural	Modified
Daily Minimum	−1.8 ± 0.0	−1.9 ± 0.0	12.8 ± 0.5*	14.8 ± 0.3*	12.1 ± 1.0	12.4 ± 1.1	72.4 ± 6.6*	63.6 ± 7.2*
Daily Maximum	3.5 (0.3)*	4.6 ± 0.3*	16.5 ± 1.5*	27.3 ± 3.1*	18.0 ± 1.7*	20.2 ± 2.3*	96.7 ± 2.5	94.3 ± 3.9
Daily Mean	1.2 ±0.3*	1.8 ± 0.3*	14.1 ± 0.6*	18.8 ± 1.5*	14.3 ± 0.8*	15.2 ± 0.9*	87.5 ± 2.4*	83.0 ± 3.0*

cantly higher daily maximum light intensity, significantly higher daily maximum and minimum substrate temperature, significantly higher maximum daily air temperature, and significantly lower daily minimum relative humidity (Fig. 2, Table 1). Particularly striking were the differences in substrate temperature (Figs. 2 and 3), where grand mean and nightly minimums were approximately 2°C higher on the altered beach but peak daytime values averaged nearly 11°C higher. Maximum substrate temperatures approached 30°C on the altered beach but always remained less than 20°C on the natural beach. In addition to more extreme values and different means for all physical variables, the altered beach showed broader distributions (Fig. 3) indicative of a more variable environment.

Both the proportion of eggs containing live embryos and total egg density at the altered beach were approximately half that of the natural beach (Table 2). Differences in proportion of eggs with live embryos were statistically significant ($p = 0.048$) but differences in total egg density were not ($p = 0.18$), probably a result of very low statistical power ($1 - \beta = 0.26$ for total density) due to the high variability inherent in the patchy distribution of eggs and the small sample sizes. Sample size power analysis indicated that increasing sample size to at least 11 samples per beach would be required to achieve conventional power of 0.8.

Discussion

Understanding the specific relationships between shoreline modification and changes in biological condition is necessary for successful shoreline management. Data from this study demonstrate that anthropogenic shoreline alteration can make shoreline environments in Puget Sound brighter, hotter, drier, and less suitable for surf smelt embryos. Although these data are limited in scope (measuring only four environmental variables at two sites at one time of year, and directly addressing only one aspect of biology), they demonstrate the potential changes in abiotic and biotic conditions that occur on modified shorelines throughout Puget Sound.

That the larger physical differences between the heavily altered and natural beaches in this study occurred during daylight indicates that changes in beach exposure to sunlight is the primary cause of differences between beaches. Removal of natural shoreline structure, including shade-providing terrestrial shoreline vegetation, can have dramatic effects on shoreline microclimate and ecology, changing average and extreme conditions and increasing variation in the physical environment, creating a harsher environment for life. Unmodi-

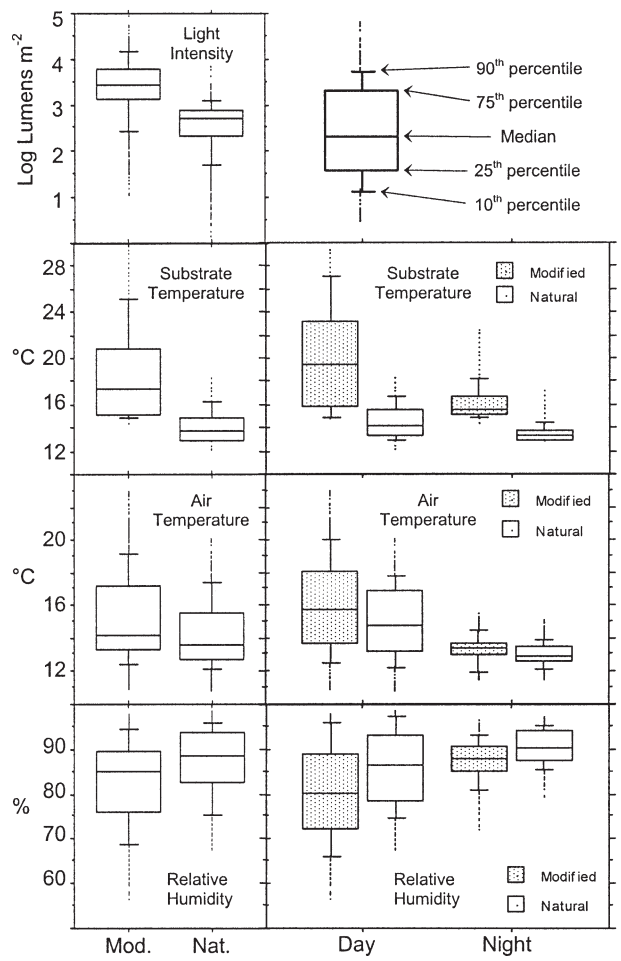

Fig. 3. Daytime light intensity and combined day and night substrate temperature, air temperature, and relative humidity at the modified and natural beaches over the entire 4-d study period (left column) and during day and night hours (right column). In right column, gray boxes are for the modified beach; white boxes are for the natural beach. Box plots show 10th, 25th, 50th (median), 75th, and 90th percentiles.

TABLE 2. Surf smelt egg density per sample and percent of eggs containing live embryos at the natural and modified beaches. Mean percentage of eggs with live embryos was significantly different between beaches ($p = 0.048$; power $(1 - \beta) = 0.74$) but total egg density was not ($p = 0.18$; power $(1 - \beta) = 0.26$).

	Smelt egg density (eggs cm^{-3}; n = 5)		Percent of smelt eggs containing live embryos (n = 5)	
	Natural	Modified	Natural	Modified
Mean (± SD)	15.7 ± 17.6	7.9 ± 4.7	49.8 ± 13.6	24.8 ± 26.3
Median	5.7	7.9	51.7	12.1
Range	1.0–35.7	2.3–14.1	32.8–63.5	1.9–59.4

fied shorelines are naturally buffered against such harsh physical conditions and are presumably more taxonomically diverse (Connell 1978) and productive (Webb et al. 1978) as a result. While empirical causal relationships between anthropogenic alterations of beach microclimate and biological condition have not been established, studies of shoreline alteration and ecology support this proposition (Attrill et al. 1999; Dugan et al. 2003), including those in or near Puget Sound (Penttila 2001; Romanuk and Levings 2003; Sobocinski 2003). Most important is that regardless of whether modified shorelines are less taxonomically diverse, productive, etc., they are certainly less natural; that is, shifted away from the conditions under which life evolved and thrived for millennia. This is an important distinction, because it is normal, natural ecological conditions (i.e., biological integrity; Karr 1991) that should be the typical baseline in environmental assessment, and it is normal, natural ecological conditions that the law often says we should protect (Angermeier and Karr 1994).

Combined with site level evaluations such as this study and others in the Puget Sound region (Penttila 2001; Romanuk and Levings 2003; Sobocinski 2003), information on the nature and extent of anthropogenic shoreline modification in Puget Sound (at least one third of the shoreline is armored; PSWQAT 2002) suggests the potential for cumulative ecological effects of altered shoreline microclimate at the landscape scale. Assessing and effectively managing for such effects will require examination of natural and anthropogenic influences of shoreline microclimate and associated biological effects at multiple spatial scales (Levin 1992; Chen et al. 1999). Management implications of such effects include minimizing further shoreline development or rehabilitating altered beaches by revegetation, bulkhead removal, etc (Williams and Thom 2001; Brennan and Culverwell 2004).

Beach Microclimate and Surf Smelt Embryos

The striking difference between the beaches in terms of the proportion of smelt eggs containing live embryos (on the altered beach approximately half that observed on the natural beach) indicates that shoreline modification has adverse effects on surf smelt embryos. The similar difference between beaches in total smelt egg density is less conclusive because it was not statistically significant, and more importantly, it is impossible to know whether reduced total density, if it is in fact real, was the result of increased egg mortality or preferential use of the natural beach by spawning adults.

Numerous biotic and abiotic factors can influence development and survival of intertidal embryos but temperature is among the most important (Frank and Leggett 1981a; DeMartini 1999). Two potential temperature related causes of the observed differences in surf smelt embryo mortality in this study are higher developmental rates in a warmer incubating environment and higher mortality resulting from thermal stress and desiccation. Because hatching is dependent on immersion by the tides, embryo development would ideally coincide with favorable tides. Similar to other upper intertidal beach spawners (Middaugh et al. 1983; DeMartini 1999), the typical incubation time for surf smelt (approximately 2 wk) does correspond with the timing of spring tide cycles. Thermal slowing of developmental rates might render embryos unprepared for the tidal inundation appropriate for hatching. Accelerated development through increased temperature could cause smelt embryos to mature early and compromise their ability to await hatching opportunities or survive after hatching. Laboratory studies from another beach spawning species, the California grunion (*Leurestes tenuis*), found that the optimum temperature range for hatching is between 16°C and 27°C, and that hatching success rapidly declines outside this range (Ehrlich and Farris 1971). California grunion also develop more rapidly and are less able to extend incubation and delay hatching at elevated incubation temperatures (Smyder and Martin 2002). Beach spawning capelin (*Mallotus villosus*) showed deterioration of larval condition with increased beach residence time of embryos (Frank and Leggett 1981b). If surf smelt embryos are similarly affected by conditions in the incubating environment, shoreline modification could have adverse effects on hatching success. Perhaps more likely to be a significant effect of shoreline modification on smelt embryos (including the lower proportions of

live smelt embryos on the altered beach in this study) is acute lethality through extreme thermal stress and desiccation. No published information on the specific thermal tolerance of surf smelt embryos exists, but a laboratory study of desiccation showed significant mortality at environmentally relevant levels of low humidity (Lee personal communication).

While this study does document significant differences in environmental conditions between modified and natural beaches and suggests that these differences affect surf smelt embryos, more detailed information on the specific environmental tolerances of smelt embryos would be useful. Expanded, systematic field studies (Frank and Leggett 1981a,b) combined with controlled laboratory experiments could provide a mechanistic understanding of the effects of shoreline alterations on surf smelt embryo survival. Such understanding could better inform site level assessments of surf smelt spawning habitat and could also provide the basis for a broader evaluation of the effects of shoreline alteration and surf smelt populations in Puget Sound as a whole.

Anthropogenic increases in low-quality spawning habitat throughout Puget Sound could shift the overall balance of surf smelt reproduction and mortality, possibly contributing to population declines. No rigorous stock assessments of surf smelt are conducted in Puget Sound, but historical beach surveys of spawning activity (Penttila 1995), and recent adult smelt catch data from nearshore surface trawls (Rice unpublished data) show uneven distribution of spawning activity and adults in the Puget Sound landscape. Whether these patterns are at all explained by anthropogenic degradation of spawning habitat is impossible to know with existing information, although the results presented here and elsewhere (Penttila 2001; Lee personal communication) suggest several important mechanisms by which reproductive success could be reduced. Explaining landscape, population-level patterns (Donovan and Thompson 2001; Feist et al. 2003) would likely require the collection of extensive demographic information on surf smelt such as spawning site fidelity or selection by adults and habitat-specific and age-specific survival. It would also require comprehensive information on the quality and distribution of potential spawning habitat in the landscape, as well as an understanding of the distribution and dynamics of surf smelt predators and prey.

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Literature Cited

Angermeier, P. L. and J. R. Karr. 1994. Biological integrity versus biological diversity as policy directives. *Bioscience* 44:690–697.

Attrill, M. J., D. T. Bilton, A. A. Rowden, S. D. Rundle, and R. M. Thomas. 1999. The impact of encroachment and bankside development on the habitat complexity and supralittoral invertebrate communities of the Thames Estuary foreshore. *Aquatic Conservation-Marine and Freshwater Ecosystems* 9:237–247.

Brennan, J. S. and H. Culverwell. 2004. Marine riparian: An assessment of riparian functions in marine ecosystems. Washington Sea Grant, Seattle, Washington. http://www.wsg.washington.edu/research/ecohealth/brennanlr.pdf (accessed 8/4/2005).

Brosofske, K. D., J. Chen, R. J. Naiman, and J. F. Franklin. 1997. Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications* 7:1188–1200.

Chen, J. Q., S. C. Saunders, T. R. Crow, R. J. Naiman, K. D. Brosofske, G. D. Mroz, B. L. Brookshire, and J. F. Franklin. 1999. Microclimate in forest ecosystem and landscape ecology—Variations in local climate can be used to monitor and compare the effects of different management regimes. *Bioscience* 49:288–297.

Colombini, I. and L. Chelazzi. 2003. Influence of marine allochthonous input on sandy beach communities. *Oceanography and Marine Biology* 41:115–119.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310.

Day, J. W., C. A. S. Hall, W. M. Kemp, and A. Yanez-Arancibia. 1989. Estuarine Ecology, 1st edition. John Wiley and Sons, New York.

Demartini, E. E. 1999. Intertidal spawning, p. 143–164. *In* M. H. Horn, K. L. M. Martin, and M. A. Chotkowski (eds.), Intertidal Fishes: Life in Two Worlds, 1st edition. Academic Press, San Diego, California.

Donovan, T. M. and F. R. Thompson. 2001. Modeling the ecological trap hypothesis: A habitat and demographic analysis for migrant songbirds. *Ecological Applications* 11:871–882.

Downing, J. 1983. The Coast of Puget Sound: Its Processes and Development, 1st edition. Washington Sea Grant, Seattle, Washington.

Dugan, J. E., D. M. Hubbard, M. D. McCrary, and M. O. Pierson. 2003. The response of macrofauna communities and shorebirds to macrophyte wrack subsidies on exposed sandy beaches of southern California. *Estuarine Coastal and Shelf Science* 58:25–40.

Ehrlich, K. F. and D. A. Farris. 1971. Some influences of temperature on the development of the grunion *Leuresthes tenuis* (Ayres). *California Fish and Game* 57:58–68.

Feist, B. E., E. A. Steel, G. R. Pess, and R. E. Bilby. 2003. The influence of scale on salmon habitat restoration priorities. *Animal Conservation* 6:271–282.

Frank, K. T. and W. C. Leggett. 1981a. Prediction of egg development and mortality rates in capelin (*Mallotus villosus*) from meteorological, hydrographic, and biological factors. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1327–1338.

Frank, K. T. and W. C. Leggett. 1981b. Wind regulation of emergence times and early larval survival in capelin (*Mallotus*

villosus). *Canadian Journal of Fisheries and Aquatic Sciences* 38:215–223.

GEIGER, R. 1965. The Climate Near the Ground. Harvard University Press, Cambridge, Massachusetts.

JEDRZEJCZAK, M. F. 2002. Spatio-temporal decay ''hot spots'' of stranded wrack in a Baltic sandy coastal system. Part I. Comparative study of the pattern: 1 type of wrack vs 3 beach sites. *Oceanologia* 44:491–512.

JOHNSON, O. W., W. S. GRANT, R. G. KOPE, K. NEELY, F. W. WAKNITZ, AND R. S. WAPLES. 1997. Status review of chum salmon from Washington, Oregon, and California. Technological Memo. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, NMFS-NWFSC-32, Seattle, Washington.

KARR, J. R. 1991. Biological integrity: A long neglected aspect of water resource management. *Ecological Applications* 1:66–84.

KELSEY, K. A. AND D. W. WEST. 1998. Riparian wildlife, p. 235–260. *In* R. J. Naiman and R. E. Bilby (eds.), River Ecology and Management: Lessons from the Pacific Coastal Ecoregion. Springer-Verlag, New York.

KNOX, G. A. 2001. The Ecology of Seashores, 1st edition. CRC Press, Boca Raton, Florida.

KOZLOFF, E. N. 1983. Seashore life of the northern Pacific Coast, 1st edition. University of Washington Press, Seattle, Washington.

KRUCKEBERG, A. R. 1991. The Natural History of the Puget Sound Country, 1st edition. University of Washington Press, Seattle, Washington.

LEVIN, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.

LEVINGS, C. D. AND G. JAMIESON. 2001. Marine and estuarine riparian habitats and their role in coastal ecosystems, Pacific region. Canadian Science Advisory Secretariat Research Document 2001/109. Ottowa, Canada.

LOOSANOFF, V. L. 1937. The spawning run of the Pacific surf smelt, *Hypomesus pretiosus* (Girard). *Internationale Revue der gesamter Hydrobiologie and Hydrographie* 36:170–183.

MACDONALD, K., D. SIMPSON, B. PAULSON, J. COX, AND J. GENDRON. 1994. Shoreline Armoring Effects on Physical Coastal Processes in Puget Sound, Washington. Washington Department of Ecology. Report 94-78. Olympia, Washington.

MARTIN, K. L. M. AND D. L. SWIDERSKI. 2001. Beach spawning in fishes: Phylogenetic tests of hypotheses. *American Zoologist* 41:526–537.

MIDDAUGH, D. P., H. W. KOHL, AND L. E. BURNETT. 1983. Concurrent measurement of intertidal environmental variables and embryo survival for the California grunion, *Leuresthes tenuis*, and Atlantic silverside, *Menidia menidia* (Pisces, Atherinidae). *California Fish and Game* 69:89–96.

MYERS, J. M., R. G. KOPE, G. J. BRYANT, D. TEEL, L. J. LIERHEIMER, T. C. WAINWRIGHT, W. S. GRANT, F. W. WAKNITZ, K. NEELY, S. T. LINDLEY, AND R. S. WAPLES. 1998. Status review of chinook salmon from Washington, Idaho, Oregon, and California. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Tech Memo NMFS-NWFSC-35. Seattle, Washington.

NAIMAN, R. J., K. L. FETHERSON, S. J. MCKAY, AND J. CHEN. 1998. Riparian Forests, p. 289–323. *In* R. J. Naiman and R. E. Bilby (eds.), River Ecology and Management: Lessons from the Pacific Coastal Ecoregion, 1st edition. Springer-Verlag, New York.

PENTTILA, D. E. 1973. Observations on some Puget Sound spawning beaches of the surf smelt (*Hypomesus pretiosus*). Supplemental Progress Report. Washington Department of Fisheries, Olympia, Washington.

PENTTILA, D. E. 1978. Studies of the surf smelt (*Hypomesus pretiosus*) in Puget Sound. Washington Department of Fisheries, Technical Report No. 42, Olympia, Washington.

PENTTILA, D. E. 1995. The WDFW's Puget Sound intertidal baitfish spawning beach survey project. Puget Sound Research '95. Conference proceedings: 235–241.

PENTTILA, D. E. 2001. Effects of shading upland vegetation on egg survival for summer-spawning surf smelt on upper intertidal beaches in Puget Sound. Puget Sound Research 2001 Conference Proceedings. http://www.psat.wa.gov/Publications/01_proceedings/sessions/oral/2a_pentt.pdf (accessed July 17, 2005).

PHILLIPS, R. C. 1984. The Ecology of Eelgrass Meadows in the Pacific Northwest: A Community Profile. U.S. Fish and Wildlife Service, FWS/OBS-84/24, Washington, D.C.

POLIS, G. A. AND S. D. HURD. 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *American Naturalist* 147:396–423.

PUGET SOUND WATER QUALITY ACTION TEAM (PSWQAT). 2002. 2002 Puget Sound Update: Eighth Report of the Puget Sound Ambient Monitoring Program. Puget Sound Water Quality Action Team. Olympia, Washington.

PUGH, P. J. A. AND H. E. MACALISTER. 1994. Acari of the supralittoral zone on sub-Antarctic South Georgia. *Pedobiologia* 38:552–565.

RAFAELLI, D. AND S. HAWKINS. 1996. Intertidal Ecology, 1st edition. Chapman and Hall, London.

RICKETTS, E. F., J. CALVIN, J. W. HEDGPETH, AND D. W. PHILLIPS. 1985. Between Pacific Tides, 5th edition. Stanford University Press, Stanford, California.

RICKLEFS, R. E. AND G. MILLER. 2000. Ecology, 4th edition. W. H. Freeman, New York.

ROMANUK, T. N. AND C. D. LEVINGS. 2003. Associations between arthropods and the supralittoral ecotone: Dependence of aquatic and terrestrial taxa on riparian vegetation. *Environmental Entomology* 32:1343–1353.

SCHAEFER, M. B. 1936. Contributions to the life history of the surf smelt (*Hypomesus pretiosus*) in Puget Sound. Washington Department of Fisheries, Biological Report 35-B. Olympia, Washington.

SIMENSTAD, C. A. 1983. The ecology of estuarine channels of the Pacific Northwest: A community profile. U.S. Fish and Wildlife Service Biological Services Program. FWS/OBS-83/05. Washington, D.C.

SIMENSTAD, C. A., B. S. MILLER, C. F. NYBLADE, K. THORNBURGH, AND L. J. BLEDSOE. 1979. Food web relationships of Northern Puget Sound and the Straight of Juan de Fuca. Office of Engineering and Technology, Office of Research and Development, U.S. Environmental Protection Agency, EPA 600/7-79-259, Washington, D.C.

SMYDER, E. A. AND K. L. M. MARTIN. 2002. Temperature effects on egg survival and hatching during the extended incubation period of California grunion, *Leuresthes tenuis*. *Copeia* 2:313–320.

SOBOCINSKI, K. L. 2003. The Impact of Shoreline Armoring on Supratidal Beach Fauna of Central Puget Sound. M.S. Thesis. University of Washington, Seattle, Washington.

THOM, R. M. AND D. K. SHREFFLER. 1994. Shoreline Armoring Effects on Coastal Ecology and Biological Resources in Puget Sound, Washington. Washington Department of Ecology, Report 94-80. Olympia, Washington.

THOMPSON, W. F. AND ASSOCIATES. 1936. The spawning of the silver smelt, *Hypomesus pretiosus*. *Ecology* 17:158–168.

U. S. FISH AND WILDLIFE SERVICE (USFWS). 1999. Endangered and threatened wildlife and plants: Determination of threatened status for bull trout in the coterminous United States. Federal Register Volume 64, number 210, pages 58909–58933, Washington, D.C.

VALIELA, I. 1995. Marine Ecological Processes, 2nd edition. Springer-Verlag, New York.

WEBB, W., S. SZAREK, W. LAUENROTH, R. KINERSON, AND M. SMITH. 1978. Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology* 59:1239–1247.

WEITKAMP, L. A., T. C. WAINWRIGHT, G. C. BRYANT, G. B. MILNER, D. J. TEEL, R. G. KOPE, AND R. S. WAPLES. 1995. Status Review of

Coho Salmon from Washington, Oregon, and California. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Tech Memo NMFS-NWFSC-24, Seattle, Washington.

WILLIAMS, G. D. AND R. M. THOM. 2001. Marine and estuarine shoreline modification issues: White paper submitted to the Washington Department of Fish and Wildlife, Washington Department of Ecology, and Washington Department of Transportation. http://wdfw.wa.gov/hab/ahg/marnrsrc.htm (accessed July 17, 2005).

YAP-CHIONGCO, J. V. 1941. *Hypomesus pretiosus*, its development and early life history. Ph.D. Dissertation. University of Washington, Seattle, Washington.

ZAR, J. H. 1996. Biostatistical Analysis, 3rd edition. Prentice-Hall, Englewood Cliffs, New Jersey.

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LEE, C. personal communication. Keystone Environmental Ltd., 320-4400 Dominion Street, Burnaby, B.C., Canada V5G-4M7.

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