Shoreline armoring disrupts marine-terrestrial connectivity across the nearshore ecotone

Sarah M. Heerhartz

A dissertation
submitted in partial fulfillment of the
requirements for the degree of

Doctor of Philosophy

University of Washington
2013

Reading Committee:
Charles A. Simenstad, Chair
Megan N. Dethier
Jason D. Toft

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Abstract

Shoreline armoring disrupts marine-terrestrial connectivity across the nearshore ecotone

Sarah M. Heerhartz

Chair of the Supervisory Committee:
Charles A. Simenstad
School of Aquatic and Fishery Sciences

As the interface between land and sea, the nearshore (marine-terrestrial) ecotone converges at the intertidal zone, where the exchange of organic materials between ecosystems occurs in the form of beach wrack: piles of seaweed, seagrass, and terrestrial plant debris suspended in water and deposited on shore as the tide ebbs. The ecological significance of algal and seagrass wrack subsidies has been well-documented for exposed-coast sandy beaches but is relatively unstudied in lower-energy and mixed-sediment beaches. In the nearshore ecotone where beaches are fringed with riparian vegetation, the potential for reciprocal subsidies between marine and terrestrial ecosystems exists. Human modification also occurs within this ecotone, particularly in the form of armoring structures for bank stabilization that physically disrupt the connectivity between ecosystems. I conducted detailed surveys of beach physical parameters, wrack and log accumulations, and supralittoral invertebrates in spring and fall over 3 years at 29 armored-unarmored beach pairs, and behavioral observations of juvenile salmon (*Oncorhcynchus* spp.) and birds at 6 pairs in Puget Sound, WA, USA. Armoring lowered the elevation of the interface between marine and terrestrial ecosystems and narrowed the width of the intertidal transition zone. Armored beaches had substantially less wrack overall and a lower proportion of terrestrial plant material in the wrack, while marine riparian zones (especially trees overhanging the beach) were an important source of wrack to unarmored beaches. Armored beaches also had far fewer logs in this transition zone. Invertebrate assemblages were significantly different between armored and unarmored beaches. Unarmored invertebrate assemblages were characterized by talitrid amphipods and adult and larval dipteran and coleopteran insects (flies and beetles, including some types that have been shown to contribute to juvenile salmon diets in other studies) and correlated with the amount of beach wrack and logs, the proportion of terrestrial material in wrack, and the maximum elevation of the beach. Shoreline type (armored or unarmored) influenced juvenile salmon distribution, however their feeding rates were relatively high at all sites, thus decreased prey availability (i.e. fewer marine riparian and/or wrack-associated insects) or altered prey resources are likely the most detrimental effects of armoring on these fish in the nearshore ecotone. Terrestrial birds, particularly Song Sparrows (*Melospiza melodia*) were commonly observed foraging among beach wrack and logs at unarmored beaches, but were largely absent from armored beaches. Based on my results, I developed a conceptual model summarizing marine-terrestrial connections across the nearshore ecotone and the disruptive effects of armoring. This study demonstrates that shoreline armoring disrupts marine-terrestrial connectivity, affecting the amount and type of organic material delivered to the nearshore ecotone in the form of wrack and logs, the abundance and taxonomic composition of supralittoral invertebrates, and the distribution and behavior of secondary consumers (juvenile salmon and birds). The results of my dissertation provide new information on relationships between physical and biological variables in the nearshore ecotone and connections between marine and terrestrial ecosystems that may be useful in informing conservation, restoration, and management actions.

Table of Contents

Chapter 1: Introduction

This chapter introduces the central and unifying themes of my dissertation: (1) ecotones, particularly between marine and terrestrial ecosystems; (2) shoreline armoring; (3) ecosystem subsidies, particularly beach wrack; and (4) conceptual models of the linkage between shoreline armoring and invertebrate communities, juvenile Pacific salmon (*Oncorhynchus* spp.), and birds. I will place my dissertation research in the context of relevant scientific literature and describe the organization, status in terms of publication of my research, and relationships between the subsequent dissertation chapters.

An ecotone is a transition area between two adjacent but different patches of landscape that often includes characteristics/attributes of both ecosystems (patches), such as the interface between riparian vegetation and marine water in coastal environments or the interface between subalpine forests and alpine tundra in mountain environments (Hansen and diCastri 1992). The ecology of an ecotone is driven by interactions between adjacent ecosystems, which are controlled by the permeability of the boundary between them and the number and strength of linkages that cross the boundary (Johnston and Naiman 1987; Naiman and Decamps 1997).

Changes to a particular ecotone linkage can fundamentally alter the structure and function of both adjacent ecosystems; alternatively, changes to ecotone characteristics (e.g. reduced permeability) can alter the linkage between ecosystems (e.g. limit the ability of a vector to move material across the ecotone). Disruptions or alterations of ecotone linkages can be affected by biotic, abiotic, or anthropogenic vectors of change. Organisms acting as ‘ecosystem engineers’ can create new landscape features: for instance, beavers build dams that create pools in otherwise flowing streams (Johnston and Naiman 1987); burrowing animals alter the physical and chemical properties of soils and cause a shift in vegetation communities (Bancroft et al. 2005; James et al. 2009); some species of oysters create reefs that add three-dimensional hard structure to otherwise soft-bottomed habitats (Padilla 2010); and the invasive cordgrass, *Spartina alterniflora*, changes sedimentation patterns and introduces new habitat structure (Callaway and Josselyn 1992), as does all estuarine emergent vegetation.

Environmental disturbances such as wildfires, storms, droughts, and floods in the short-term and climate change, glacial advance or retreat, and tectonic activity over the long-term can provide mechanisms for alteration of ecotone linkages; these may result in new geographical positions of ecotones, new ecotones between disturbed and undisturbed landscape patches, increased habitat diversity by successional development post-disturbance, and/or space for species invasions. Wildfires can influence the altitude and latitude, successional development, and species composition of vegetation communities in alpine treeline – tundra ecotones (Stueve et al. 2009), forest – grassland ecotones (Norman and Taylor 2005; Peterson and Reich 2008), chapparal/oak – mixed conifer ecotones (Franklin 2009), and riparian – aquatic ecotones (Jackson and Sullivan 2009). Floods periodically connect rivers to floodplains, allowing exchange of nutrients, organic material, and sediments across ecotone boundaries, maintaining spatio-temporal heterogeneity, and adding habitat diversity (Ward et al. 1999; Ward and Wiens 2001). Local weather anomalies, such as drought or heavy precipitation, or regional climate phenomena such as El Nino/Southern Oscillation (ENSO), create habitat variability and disturbance that can alter species distributions or fluxes of energy, inorganic and organic materials, and organisms across boundaries, allow invasion by non-native species, or create landscape patches at different stages of successional development (League and Veblen 2006; Shuman et al. 2009). Geologic activity at ecotone boundaries can affect their position or persistence; for example, shoreline erosion can cause landward migration of the upper intertidal ecotone (Fenster and Hayden 2007).

Anthropogenic activity also can be a major driver of change across ecotones. Human land use practices including agriculture, livestock grazing (Wasson and Woolfolk 2011), and removal of native vegetation/deforestation (Minchinton and Bertness 2003; Lavigne and Gunnel 2006) alter landscapes in a number of ways, including increasing the area of bare ground, reducing species richness of native plants, increasing non-native plant cover, and shifting the geographic location and/or species composition of ecotone boundaries or creating novel ecotones between disturbed and undisturbed patches. Regulation of river flows and flood control in the form of dams, dikes, and diversions impacts ecotone structure and functioning by changing the permeability of boundaries and the connectivity between landscape patches. Reduced flooding decreases the exchange of sediments and nutrients across ecotone boundaries and dampens spatio-temporal heterogeneity that would normally maintain habitat diversity (Ward et al. 1999; Ward and Wien 2001). In marsh – upland ecotones, reduction of freshwater flows reduces ecotone width, alters salinity gradients and tidal channel geomorphology (Davis et al. 2005), reduces habitat space to support native ecotone specialists, decreases native marsh plant richness and can cause a seaward shift of the entire ecotone in coastal marsh systems (Wasson and Woolfolk 2011). Modern control of forest fires has resulted in both reduction of fire frequency and extent burned, causing shifts in the dominant plant types in montane forest ecotones (Franklin et al. 2005; Mast and Wolf 2006) and allowing forests to expand into meadows or alpine tundra, shifting the position and/or altitude of the ecotone boundary and decreasing the size of adjacent patches (Norman and Taylor 2005). Pollution can cause functional changes in aquatic ecotones: contamination with heavy metals associated with urban runoff inhibits the nursery function of estuaries (Courrat et al. 2009), and nutrient pollution enables invasion of novel species into marsh habitats (Minchinton and Bertness 2003). 'Grooming' or 'cleaning' at recreational beaches removes deposited marine wrack, seagrass, and terrestrial plant debris from the upper intertidal ecotone, disrupting pathways of decomposition and nutrient exchange between marine and terrestrial ecosystems and altering the compostition of invertebrate communities and food availability for a variety of consumers (Dugan et al. 2003, Gheskiere et al. 2005).

As the interface between land and sea, the nearshore (marine-terrestrial) ecotone converges at the intertidal zone, where the exchange of organic materials between ecosystems occurs in the form of beach wrack: piles of seaweed, seagrass, and terrestrial plant debris suspended in water and deposited on shore as the tide ebbs. Along the barrier beaches of Puget Sound, WA, USA this ecotone in its undisturbed condition is characterized by riparian vegetation (trees and shrubs in soils comprising the bank just above the beach) and accumulation along the upper shore of logs and beach wrack (composed of a mix of debris from marine macrophytes, algae, and terrestrial plants); the seaward, lower tidal elevation ecosystem is an active beach face composed of relatively bare sediment (typically a mix of sand, pebbles, and cobbles), and algae and seagrass beds in the low intertidal to subtidal zones. The shoreline of Puget Sound is comprised of many different geomorphic land forms, including stream deltas, embayments, and salt marshes, which may also accumulate wrack; however my dissertation research is focused on barrier beaches bordered with riparian vegetation.

Within ecotones, nutrients, detritus, and organisms from adjacent ecosystems converge, and some may cross the ecotone into the adjacent ecosystem. Ecosystem subsidies consist of organic material that crosses ecosystem boundaries and becomes available to consumers from the adjacent ecosystem. Ecosystem subsidies increase primary productivity and/or the density and diversity of consumers in the recipient habitat (Polis et al. 1997) and can be important in structuring and maintaining food web linkages (Nakano et al. 1999) and ecosystem functions such as habitat quality for many species of ecological or economic importance (Helfield and Naiman 2001).

Beach wrack constitutes a subsidy, consisting of organic material from marine and terrestrial ecosystems that by its concentration in this nearshore ecotone provides food and shelter for primary consumers, which in turn are consumed by organisms both landward and seaward of the wrack zone. Wrack plays an important role in shaping beach invertebrate communities (Colombini et al. 2000; Cowles et al 2009; MacMillan and Quijón 2012), and wrack-associated invertebrates are key players in nutrient cycling and decomposition (Griffiths and Stenton-Dozey 1981; Mews et al. 2006; Lastra et al. 2008).

While many studies have established the importance of marine macroalgae and seagrasses as subsidies to sandy beaches and adjacent terrestrial ecosystems (Polis and Hurd 1996; Dugan et al. 2003; Gonçalves and Marques 2011; Mellbrand et al. 2011), few have examined the role of a reciprocal subsidy from the land to the beach. Reciprocal subsidization may be minimal in many marine open coast systems, but in estuarine systems fringed with riparian vegetation there can be comparable exchange of nutrients, detritus, and prey items between estuarine and terrestrial ecosystems. Such reciprocal subsidization between aquatic and terrestrial ecosystems occurs between freshwater streams and adjacent riparian ecosystems (Nakano and Murakami 2001; Baxter et al. 2005), and it may also be important in estuarine nearshore ecotones like those in Puget Sound.

Ecotones are usually not characterized by conspicuous boundaries (Naiman and Decamps 1997; Polis and Hurd 1997). Changing the type of boundary between two ecosystems can affect the distribution of organisms within and across the ecotone. For example, clear-cutting in forests produces lower edge complexity and a narrower ecotone width than natural disturbances, with consequences for vegetation communities (Braithwaite and Mallik 2012), and birds in alpine forests that occupy complex edge vegetation in the forest – pasture ecotone avoid lower-complexity forest – ski-run edges (Laiolo and Rolando 2005). Shoreline armoring, referring to any kind of artificial hard structure emplaced to prevent natural erosion of shoreline sediments, imposes a distinct barrier within the gradient of the intertidal zone and thus can significantly alter ecotone dynamics. Shoreline armoring reduces ecotone complexity and connectivity between patches landward and seaward of its location, disrupting inputs and exchange of materials, nutrients and prey resources between land and sea. Recent studies have shown multiple physical and biological impacts of armoring in open coast sandy beach ecosystems (Brown and McLachlan 2002; Schlacher et al. 2007; Dugan et al. 2008; Defeo et al. 2009; Bernatchez and Fraser 2012), rocky intertidal zones (Chapman 2003; Clynick et al. 2008), intertidal mudflats (Morley et al. 2012), and freshwater lakes (Tabor et al. 2011), but relatively few studies have investigated the effects of armoring on intertidal mixed sand and gravel barrier beaches (Rice et al. 2006; Sobocinski et al. 2010). While there is some evidence that shoreline armoring changes the physical properties of beaches (Nordstrom 1992; Mason and Coates 2001; Miles et al. 2001; Leschine 2010) and alters upper intertidal invertebrate communities (Romanuk and Levings 2003, Sobocinski et al. 2010), the relationships between physical and biological effects of armoring in estuarine nearshore environments are poorly studied.

Armoring may reduce the actual amount of space within the nearshore ecotone, for example if it involves removal of a particular landscape unit such riparian vegetation, or reduction in the size of a particular habitat as in the case of a vertical seawall emplaced on the beach face that truncates the intertidal gradient. Shoreline armoring may alter the features of available habitat space, for example a vertical seawall encroaching on the upper intertidal zone may increase reflected wave energy and introduce novel hard vertical substrates, while removal of native supralittoral vegetation may limit the exchange of nutrients, detritus, or riparian invertebrates and reduce shading of the upper beach, altering the microclimate (Romanuk and Levings 2003; Rice 2006).

My dissertation was motivated by two primary questions: (1) Are reciprocal subsidies important components of the nearshore ecotone? and, (2) How does shoreline armoring affect marine-terrestrial connectivity across the nearshore ecotone? In particular, I compared the flux of organic matter and organisms between marine and terrestrial ecosystems in the upper intertidal ecotone between armored and unarmored beaches and the relationship between environmental variables and biological communities. This research was specifically focused on marine riparian and wrack-associated invertebrates, and secondary consumers from marine (juvenile salmon) and terrestrial (birds) ecosystems.

Study approach

All sampling was carried out at armored-unarmored beach pairs throughout central and south Puget Sound, with armored shorelines considered as treatments and adjacent unarmored shorelines as references, although the adjacent ‘references’ may be impacted by concomitant shoreline development. I sampled wrack, logs, and associated invertebrates at 29 pairs of beaches over the course of three years, providing broad spatial replication. Juvenile salmon and birds were surveyed at fewer sites but still maintained the armored-unarmored pairing design that allowed for direct comparison of behavior, feeding rates, and habitat use by shore type.

Conceptual models of the effects of shoreline armoring in the nearshore ecotone and organization of dissertation chapters

Conceptual models were developed to illustrate known and potential effects of shoreline armoring and to identify knowledge gaps in need of investigation (Figs. 1-3). They are designed to capture the physical effects of armoring, which influence the potential sources of and accumulation space for beach wrack and driftwood logs, and determine the type and amount of habitat available for beach and marine riparian biota. The components of the conceptual model showing the physical effects (except bluff erosion) of shoreline armoring (Fig. 1) are discussed in Chapter 2, *Effects of shoreline armoring on beach wrack subsidies to the nearshore ecotone in an estuarine fjord,* with focus on the relationship between physical and biological variables. This chapter has been accepted with minor revisions by *Estuaries and Coasts*, with revisions completed. Results showed that armoring disrupts beach wrack subsidies to estuarine nearshore ecosystems. Specifically, we found that in terms of both biomass and abundance, there was less wrack at armored beaches and a lower proportion of terrestrial plant material in the wrack. Logs were rare at armored beaches but present at all unarmored beaches. Armored beaches were narrower, had lower maximum elevations, and coarser upper beach sediments. Detailed characterizations of sediments and wave measurements were collected but are not presented here; these data are being prepared as a separate manuscript for publication (Ogston et al., in prep). In this work, we were able to quantify an impact of armoring on local wave heights but not on beach morphology (slope and grain size) that is extremely variable on these mixed-grain-size beaches. In this glaciated landscape, it appears that the variability of source sediment and antecedent geomorphology that produced subtle differences in factors such as substrate composition, fetch and shore aspect, and proximity to feeder bluffs make it almost impossible to define pairs of beaches in which we can isolate the impacts of armoring. Physical responses to shoreline armoring in need of investigation that were identified in Fig. 1 (represented by italic text followed with a "?") and addressed in my dissertation research include: erosion of upper beach sediments in front of armoring, altered sediment distribution, changes in wave dynamics, and reduced accommodation space. The first two of these were addressed through beach profiles and sediment grain size analysis; while we found no differences in beach slope, we did find that wrack line sediments contained more cobbles (and thus were coarser) at armored beaches, indicating changes in sediment distribution and suggesting that finer sediments may be eroded from the upper beach below armoring structures. Wave dynamics were addressed through wave gauge studies at two armored-unarmored beach pairs (Ogston et al., in prep) not included in my dissertation that showed increased wave heights at armored beaches. Wave dynamics were also indirectly addressed in a wrack tube experiment (see discussion of Chapter 3, below), where many of our experimental tubes were destroyed or lost at armored beaches. Accommodation space was addressed in terms of wrack and log deposition, which were reduced at armored beaches; sediment deposition was not addressed. Potential responses in the conceptual model that remain in need of investigation and were not addressed here include altered beach hydrodynamics or altered swash zone processes.

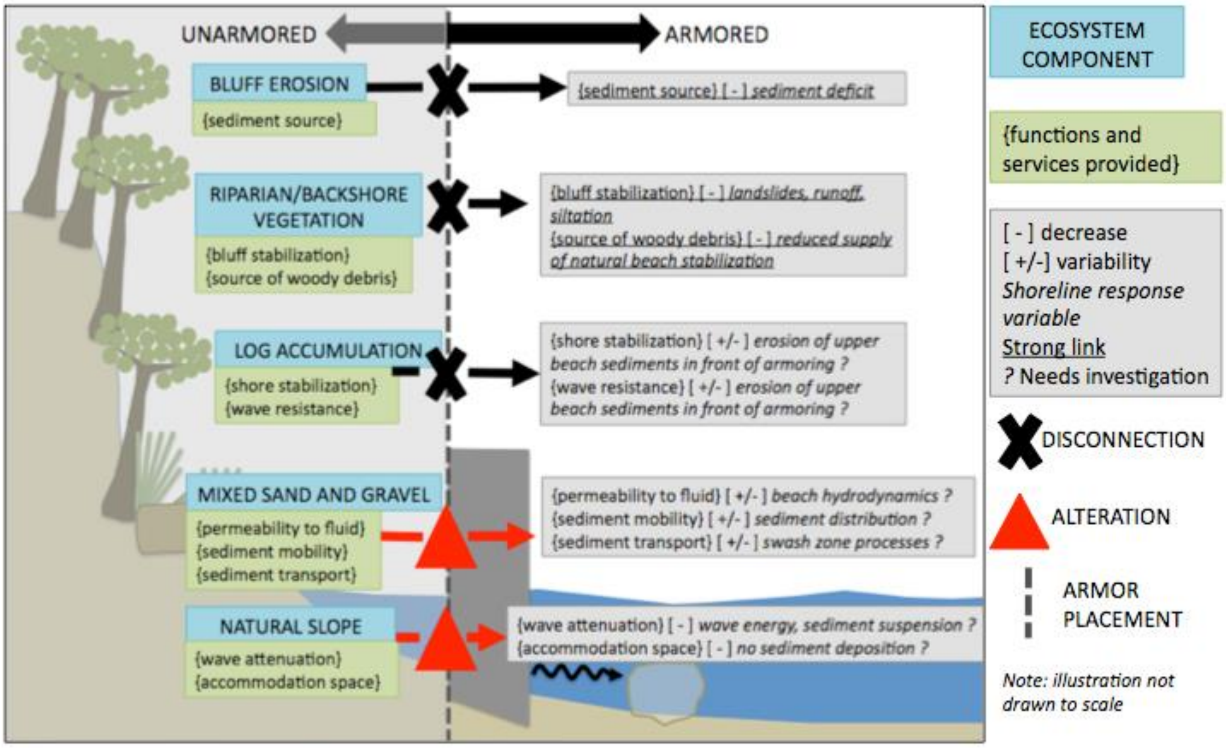

Figure 1 Conceptual model of the physical effects of shoreline armoring.

The potential effects of shoreline armoring on juvenile salmon and birds can be illustrated in more focused conceptual models (Figs. 2 and 3, respectively). These effects were investigated in terms of potential prey resources in Chapter 3, *Shoreline armoring disrupts wrack-associated invertebrate communities in the nearshore ecotone,* and juvenile salmon behavior and movement in Chapter 4, *Movement patterns and feeding behavior of juvenile salmon (Oncorhynchus spp.) along armored and unarmored estuarine shorelines*. I did not develop a specific conceptual model for Chapter 3, which focused on invertebrates associated with beach wrack; instead this chapter is represented conceptually in both the juvenile salmon (Fig. 2) and bird (Fig. 3) models. Chapter 3 was prepared as a publishable manuscript, examining the effects of disrupted marine-terrestrial linkages caused by armoring and the influence of beach wrack in shaping upper intertidal invertebrate communities, specifically: the relationships between environmental parameters associated with wrack and logs (e.g., biomass and wrack composition, width of log line) and talitrid and insect assemblages, the abundance and diversity of mobile invertebrates, and the role of talitrid amphipods and other invertebrates in wrack decomposition. Overall, armored beaches had fewer talitrid amphipods and insects than unarmored beaches, and unarmored invertebrate assemblages were correlated with wrack biomass, the proportion of terrestrial material in the wrack, the maximum elevation of the beach, and the width of the log line. Chapter 4 has been submitted to *Environmental Biology of Fishes* and is currently in review. In it, we compared movement patterns and feeding rates of juvenile salmon along armored and unarmored shorelines. Juvenile salmon were more frequently observed at unarmored beaches, indicating that armoring affects their distribution. Feeding rates were similar at armored and unarmored beaches, thus we suggest that armoring affects juvenile salmon by reduction of marine riparian prey inputs (i.e. terrestrial insects), as demonstrated in Chapter 3. Responses of juvenile salmon to shoreline armoring that are in need of investigation (Fig. 2) that were addressed in my dissertation include: reduced food web connectivity; and, changes in feeding and other behaviors. Armored beaches supported fewer riparian and wrack-associated insects as a result of reduced habitat for these organisms (less wrack, fewer logs, removal of riparian vegetation) or altered fluxes across the nearshore ecotone. Juvenile salmon were observed less frequently along armored beaches, but movement rates, feeding rates, and path sinuosity did not differ significantly between armored and unarmored beaches, although the range of movement rates and path sinuosity was greater at unarmored beaches. Further investigation is needed to address whether armored beaches present increased predation risk to juvenile salmon, whether the lower numbers of potential insect prey found along the upper shore at armored beaches translate to fewer insects available on the surface of the water, whether there is an energetic cost of foraging in deeper water along armored shorelines (e.g. if prey are more rare but feeding rates are consistent), and whether any of these potential effects of armoring (or all of them combined) influence growth rates and survival of juvenile salmon.

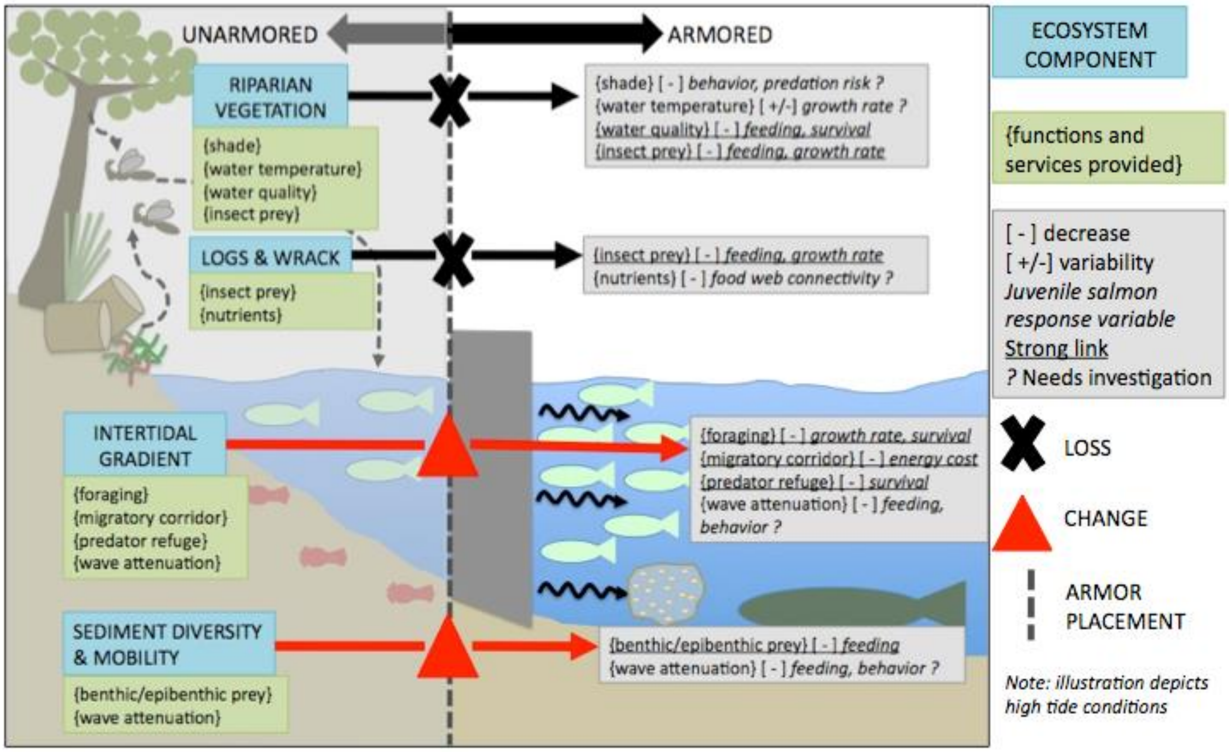

Figure 2 Conceptual model of potential linkages between shoreline armoring and juvenile salmon.

Potential linkages between shoreline armoring and birds (Fig. 3) and are discussed in Chapter 2 in terms of biogenic habitat (beach wrack and logs), in Chapter 3 in terms of prey resources and in Chapter 5, *Differences in abundance and behavior of terrestrial birds on armored and unarmored beaches,* in terms of actual foraging behaviors of birds. This chapter was prepared as a publishable manuscript documenting bird use of upper intertidal habitats, with particular focus on differences between armored and unarmored beaches. Few studies have documented the value of nearshore marine beaches for terrestrial bird species. I demonstrated that songbirds forage in beach wrack along unarmored shores but are rarely observed along armored shores and that overall birds spend a higher proportion of time foraging at unarmored beaches than at armored beaches. Responses of terrestrial birds to shoreline armoring in need of investigation (Fig. 3) that were addressed here include: reduced predator refuge habitats; changes in feeding behaviors; and reduced food web connectivity. Because armored shorelines generally lacked both riparian vegetation and logs, they provide significantly less shade and cover for small songbirds, thus representing loss of predator refuge habitats. Feeding behaviors were significantly lower at armored beaches for songbirds (as well as all birds observed), likely due to the loss of upper beach foraging habitats (beach wrack and logs) and the reduced prey available (insects, talitrid amphipods). Terrestrial birds were far less likely to find suitable prey and foraging habitats on armored beaches, therefore armoring reduces food web connectivity across the nearshore ecotone for these organisms. Potential effects of shoreline armoring on diving birds were not addressed and are in need of investigation. Forage fish eggs, and whether or not these represent a seasonal food resource for foraging birds is another component of the model that was not addressed in my dissertation research. Prey quality was not specifically addressed in this study, although if feeding preferences are any indication prey quality is likely lower at armored beaches for terrestrial songbirds. Whether or not the behavioral responses to armoring and the reduced prey resources at armored beaches have consequences for reproductive success, growth, and/or survival of birds remains in need of investigation.

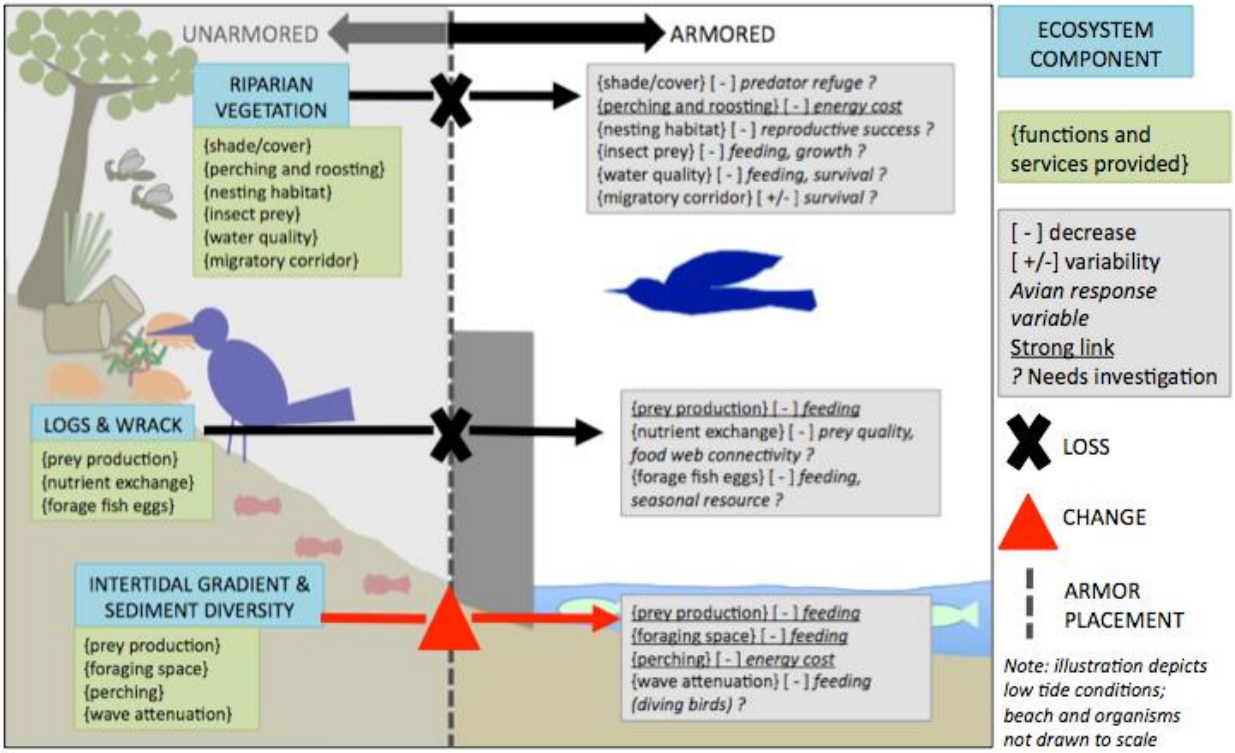

Figure 3 Conceptual model of potential linkages between shoreline armoring and birds, with emphasis on terrestrial songbirds but also including shore and water birds.

In Chapter 6, *Comprehensive conclusion, development of conceptual model of effects of armoring on marine-terrestrial linkages*, I synthesized the results of all components of my dissertation into a summary model of the effects of shoreline armoring on the nearshore ecotone. This chapter will eventually be written as a synthetic paper for publication. Connections between beach wrack and the primary consumers it supports were addressed; the disruptive effects of armoring on wrack-associated and marine riparian invertebrate communities, and consequences for secondary consumers in estuarine and terrestrial ecosystems were visually illustrated and supported with empirical evidence.

References

Bancroft, W.J., M.J. Garkaklis, and J.D. Roberts. 2005. Burrow building in seabird colonies: a soil-forming process in island ecosystems. Pedobiologia 49: 149–165.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Bernatchez, P. and C. Fraser. 2012. Evolution of coastal defence structures and consequences for beach width trends, Quebec, Canada. Journal of Coastal Research 28: 1550-1566.

Braithwaite, N. and A. Mallik. 2012. Edge effects of wildfire and riparian buffers along boreal forest streams. Journal of Applied Ecology 49: 192-201.

Brown, A. and A. McLachlan. 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environmental Conservation 29: 62-77.

Bustamante, R. H. and G. M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196: 1–28.

Callaway, J.C. and M.N. Josselyn. 1992. The introduction and spread of smooth cordgrass (*Spartina alterniflora*) in south San Francisco Bay. Estuaries 15: 218-226.

Chapman, M.G. 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Marine Ecology Progress Series 264: 21-29.

Clynick, B. G., M.G. Chapman, and A. J. Underwood. 2008. Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33: 140-150.

Colombini, I., A. Aloia, M. Fallaci, G. Pezzoli, and L. Chelazzi. 2000. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. Marine Biology 136: 531-541.

Courrat, A., J. Lobry, D. Nicolas, et al. 2009. Anthropogenic disturbance on nursery function of estuarine areas for marine species. Estuarine, Coastal and Shelf Science 81: 179-190.

Cowles, A., J.E. Hewitt, and R.B. Taylor. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. Marine Ecology Progress Series 384: 175-185.

Davis, S.M., D.L. Childers, J.J. Lorenz, H.R. Wanless, and T.E. Hopkins. 2005. A conceptual model of ecological interactions in the mangrove estuaries of the Florida Everglades. Wetlands 25: 832-842.

Defeo, O., A. McLachlan, D.S. Schoeman, T.A. Schlacher, J. Dugan, A. Jones, M. Lastra, and F. Scapini. 2009. Threats to sandy beach ecosystems: A review. Estuarine Coastal and Shelf Science 81: 1-12.

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 58S: 25-40.

Dugan, J.E., D.M. Hubbard, I.F. Rodil, D.L. Revell, S. Schroeter. 2008. Ecological effects of coastal armoring on sandy beaches. Marine Ecology 29: 160-170.

Fenster, M.S. and B.P. Hayden. 2007. Ecotone displacement trends on a highly dynamic barrier island: Hog Island, Virginia. Estuaries and Coasts 30: 978-988.

Franklin, J. 2009. Vegetation dynamics and exotic plant invasion following high severity crown fire in a southern California conifer forest. Plant Ecology 207: 281-295.

Franklin, J., A.D. Syphard, H.S. He, and D.J. Mladenoff. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. Ecosystems 8: 885-898.

Gheskiere, T., M. Vincx, J.M. Weslawski, F. Scapini, and S. Degraer. 2005. Meiofauna as descriptor of tourism-induced changes at sandy beaches. Marine Environmental Research 60: 245-265.

Gonçalves, S.C. and J.C. Marques. 2011. The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. Estuarine, Coastal and Shelf Science 95: 165-177.

Griffiths, C.L. and J. Stenton-Dozey. 1981. The fauna and rate of degradation of stranded kelp. Estuarine, Coastal and Shelf Science 12: 645-653.

Hansen, A. and F. diCastri, eds. 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. New York: Springer-Verlag.

Helfield, J.M. and R.J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82: 2403-2409.

Ince, R., G.A. Hyndes, P.S. Lavery, and M.A. Vanderklift. 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuarine Coastal and Shelf Science 74: 77-86.

Jackson, B.K., S. Mažeika, and P. Sullivan. 2009. Influence of wildfire severity on riparian plant community heterogeneity in an Idaho, USA wilderness. Forest Ecology and Management 259: 24–32.

James, A.I., D.J. Eldridge, and B.M. Hill. 2009. Foraging animals create fertile patches in an Australian desert shrubland. Ecogeography 32: 723-732.

Johnston, C.A., and R.J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1: 47-57.

Laiolo, P. and A. Rolando. 2005. Forest bird diversity and ski-runs: a case of negative edge effect. Animal Conservation 8: 9-16.

Lastra, M., H.M. Page, J.E. Dugan, D.M. Hubbard, and I.F. Rodil. 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Marine Biology 154: 163-174.

Lavigne, F. and Y. Gunnell. 2006. Land cover change and abrupt environmental impacts on Javan volcanoes, Indonesia: a long-term perspective on recent events. Regional Environmental Change 6: 86-100.

League, K. and T. Veblen. 2006. Climatic variability and episodic Pinus ponderosa establishment along the forest-grassland ecotones of Colorado. Forest Ecology and Management 228: 98-107.

Leschine, T.M. 2010. Human dimensions of nearshore restoration and shoreline armoring, with application to Puget Sound, in Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds., 2010, Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigation Report 2010-5254, pp 103-113.

Lloyd, A.H., T.S. Rupp, C.L. Fastie, and A.M. Starfield. 2002. Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. Journal of Geophysical Research-Atmospheres 108 (D2) art. no. 1861.

Markgraf, V. and U.M. Huber. 2010. Late and postglacial vegetation and fire history in southern Patagonia and Tierra del Fuego. Palaeography Palaeoclimatology Palaeoecology 297: 351-366.

Mason, T. and T.T. Coates. 2001. Sediment transport processes on mixed beaches: a review for shoreline management. Journal of Coastal Research 17: 645-657.

Mast, J.N. and J.J. Wolf. 2006. Spatial patch patterns and altered forest structure in middle elevation versus upper ecotonal mixed-conifer forests, Grand Canyon National Park, Arizona, USA. Forest Ecology and Management 236: 241–250.

Mellbrand, K., P.S. Lavery, G. Hyndes, and P.A. Hamback. 2011. Linking land and sea: different pathways for marine subsidies. Ecosystems 14: 732-744.

Mews, M., M. Zimmer, and D.E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328: 155–160.

Miles, J.R., P.E. Russel, and D.A. Huntley. 2001. Field measurements of sediment dynamics in front of a seawall. Journal of Coastal Research 17: 195-206.

Minchinton, T.E. and M.D. Bertness. 2003. Disturbance-mediated competition and the spread of *Phragmites australis* in a coastal marsh. Ecological Applications 13: 1400-1416.

Morley, S.A., J.D. Toft, and K.M. Hanson. 2012. Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound urban estuary. Estuaries and Coasts 35: 774-784.

Naiman, R.J., and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecological Systems 28: 621-658.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999. Terrestrial-aquatic linkages: Riparian arthropod inputs alter trophic cascades in a stream food web. Ecology 80: 2435-2441.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98: 166-170.

Nordstrom, K.F. 1992. Estuarine beaches: an introduction to the physical and human factors affecting use and management of beaches in estuaries, lagoons, bays, and fjords. Elsevier Applied Science. New York, USA, 225 p.

Norman, S.P. and A.H. Taylor. 2005. Pine forest expansion along a forest-meadow ecotone in northeastern California, USA. Forest Ecology and Management 215: 51-68.

Padilla, D.K. 2010. Context-dependent impacts of a non-native ecosystem engineer, the Pacific oyster *Crassostrea gigas*. Integrative and Comparative Biology 50: 213-225.

Peterson, D.W. and P.B. Reich. 2008. Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecotone. Plant Ecology 194: 5-16.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289-316.

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.

Rice, C.A. 2006. Effects of shoreline modification on a northern Puget Sound beach: microclimate and embryo mortality in surf smelt (*Hypomesus pretiosus*). Estuaries and Coasts 29: 63-71.

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.

Schlacher, T.A., J.E. Dugan, D.S. Shoeman, M. Lastra, A. Jones, F. Scapini, and A. McLachlan. 2007. Sandy beaches at the brink. Diversity and Distributions 13: 556-560.

Shuman, B., A.K. Henderson, C. Plank, I. Stefanova, and S.S. Ziegler. 2009. Woodland-to-forest transition during prolonged drought in Minnesota after ca. AD 1300. Ecology 90: 2792-2807.

Sobocinski, K.L.; Cordell, J.R. and Simenstad, C.A. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuaries and Coasts 33: 699-711.

Stueve, K.M., D.L. Cerney, R.M. Rochefort, and L.L. Kurth. 2009. Post-fire establishment patterns at the alpine treeline ecotone: Mount Rainier National Park, Washington. Journal of Vegetation Science 20: 107-120.

Tabor, R. A., K.L. Fresh, R.M. Piaskowski, H.A. Gearns, and D. B. Hayes. 2011. Habitat use by juvenile Chinook salmon in the nearshore areas of Lake Washington: effects of depth, lakeshore development, substrate, and vegetation. North American Journal of Fisheries Management 31: 700-713.

Ward, J.V., K. Tockner, and F. Schiemer. 1999. Biodiversity of floodplain river ecosystems: ecotones and connectivity. Regulated Rivers: Research and Management 15: 125–139.

Ward, J.V. and J.A. Wiens. 2001. Ecotones of riverine ecosystems: Role and typology, spatio-temporal dynamics, and river regulation. Ecohydrology and Hydrobiology 1: 25-36.

Wasson, K. and A. Woolfolk. 2011. Salt marsh-upland ecotones in central California: vulnerability to invasions and anthropogenic stressors. Wetlands 31: 389-402.

Williams, J.W., B.N. Shuman, T. Webb III, P.J. Bartlein, and P.L. Leduc 2004. Late-Quaternary vegetation dynamics in North America: scaling from taxa to biomes. Ecological Monographs 74: 309–334.

Chapter 2: Effects of shoreline armoring on beach wrack subsidies to the nearshore ecotone in an estuarine fjord

Sarah M. Heerhartz[1], Megan N. Dethier[2], Jason D. Toft[1], Jeffery R. Cordell[1], and Andrea S. Ogston[3]

[1] School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195 USA

[2] Friday Harbor Laboratories and Biology Dept., University of Washington, 620 University Road, Friday Harbor, WA 98250 USA

[3] School of Oceanography, University of Washington, Box 357940, Seattle, WA 98195 USA

Corresponding author: S. M. Heerhartz
Email: sarmarie@uw.edu
Tele: 001 206 948 7206
Fax: 001 206 685 7471

Abstract

The ecological significance of algal and seagrass wrack subsidies has been well-documented for exposed-coast sandy beaches but is relatively unstudied in lower-energy and mixed-sediment beaches. In marine nearshore environments where beaches are fringed with riparian vegetation, the potential for reciprocal subsidies between marine and terrestrial ecosystems exists. Within the marine-terrestrial ecotone, upper intertidal “wrack zones” accumulate organic debris from algae, seagrass, and terrestrial plant sources and provide food and habitat for many organisms. Human modification also occurs within this ecotone, particularly in the form of armoring structures for bank stabilization that physically disrupt the connectivity between ecosystems. We conducted detailed wrack and log surveys in spring and fall over 3 years at 29 armored-unarmored beach pairs in Puget Sound, WA, USA. Armoring lowered the elevation of the interface between marine and terrestrial ecosystems and narrowed the width of the intertidal transition zone. Armored beaches had substantially less wrack overall and a lower proportion of terrestrial plant material in the wrack, while marine riparian zones (especially trees overhanging the beach) were an important source of wrack to unarmored beaches. Armored beaches also had far fewer logs in this transition zone. Thus, they lacked biogenic habitat provided by logs and riparian wrack as well as the organic input used by wrack consumers. Results such as these that demonstrate armoring-associated loss of connectivity across the marine-terrestrial ecotone may be useful in informing conservation, restoration, and management actions.

Keywords: beach wrack, shoreline armoring, ecotone, marine riparian, logs

Introduction

Humans are major vectors of environmental change, including alteration of physical structures and ecological functions within ecosystems. In coastal environments, shoreline armoring is one example of anthropogenic disturbance that is likely to increase in the face of sea level rise and climate change. Shoreline armoring refers to any kind of artificial structure emplaced to prevent natural erosion of shoreline sediments. Examples include vertical concrete seawalls or riprap (boulder) retaining walls parallel to shore. Such structures may enable development of valuable waterfront property or protect existing coastal infrastructure. Recent studies have shown multiple physical and biological impacts of armoring in open coast sandy beach ecosystems (Brown and McLachlan 2002; Schlacher et al. 2007; Dugan et al. 2008; Defeo et al. 2009; Bernatchez and Fraser 2012), rocky intertidal zones (Chapman 2003; Clynick et al. 2008), intertidal mudflats (Morley et al. 2012), and freshwater lakes (Tabor et al. 2011), but relatively few studies have investigated the effects of armoring on intertidal mixed sand and gravel beaches (Rice et al. 2006; Sobocinski et al. 2010).

Armoring structures are often placed at the interface, or ecotone, between marine and terrestrial ecosystems. An ecotone is a transition area that connects two adjacent but different patches of landscape, such as riparian vegetation and marine habitats in coastal environments (Naiman and Decamps 1997; Levings and Jamieson 2001; Brennan and Culverwell 2004) or subalpine forests and alpine tundra in mountain environments (Hansen and DiCastri 1992). Changes in ecotones can alter the structure and function of both adjacent ecosystems. Ecotone ecology is driven by interactions between the two systems including the permeability of their boundary, and by the number and strength of linkages that cross the boundary (Johnston and Naiman 1987; Naiman and Decamps 1997). Coastal marine-terrestrial ecotones have received little attention in the scientific literature, despite their value for both human uses and as habitat for many migratory and resident organisms (Polis and Hurd 1996; Rose and Polis 1998; Mellbrand et al.

2011). Landscape fragmentation caused by anthropogenic modification such as armoring changes the permeability of the marine-terrestrial boundary, reducing connectivity (Romanuk and Levings 2003; Sobocinski et al. 2010), with direct and indirect consequences for beach biota (Chapman 2003). Despite its position at the interface of aquatic and terrestrial realms, the consequences of armoring in terms of cumulative effects for marine nearshore ecology are particularly poorly studied.

In sandy beach habitats on wave-exposed coasts, the importance of subsidies from marine wrack and terrestrial organic debris has been demonstrated (Polis and Hurd 1996; Dugan et al. 2003; Cowles et al. 2009). The role of ecosystem subsidies in mixed-sediment or more wave-protected coastal environments has received less study (Romanuk and Levings 2003; Orr et al. 2005), and the effects of shoreline armoring on subsidies in these environments is virtually unknown. Furthermore, most beach subsidy studies have focused on marine-derived wrack (algal and eelgrass), although terrestrial organic detritus may also be important (Romanuk and Levings 2003), especially in embayments and estuaries. Inputs of marine and terrestrial organic debris to intertidal environments provide food and habitat space for many invertebrates, including talitrid amphipods, insects and worms. These intertidal invertebrates can act as decomposers or consumers contributing to nutrient cycling and retention (Robertson and Lucas 1983; Mann 1988; Zimmer et al. 2004; Mews et al. 2006), and can represent an important transfer of marine and terrestrial nutrients when consumed by mobile predators such as birds, fish, and mammals (Robertson and Lenanton 1984; Wright et al. 2013). Wrack zones can be important foraging habitats for shorebirds feeding on talitrid amphipods, insects and other invertebrates (Kirkman and Kendrick 1997; Dugan et al. 2003; Hubbard and Dugan 2003). In addition, upper intertidal wrack zones are important spawning habitats for some forage fishes (Rice 2006; Tonkin et al. 2007; Quinn et al. 2012), which in turn provide food for many species of birds, fish, and mammals. Insects that develop in the wrack zone and are carried by wind onto the surface of nearshore waters can become available to subsidize the diets of fish feeding along shore (Toft et al. 2007; Duffy et al. 2010; Romanuk and Levings 2010).

In this study, we used paired armored and unarmored beaches across a broad spatial range to quantitatively assess effects of armoring on marine-terrestrial ecotone linkages in the mixed-sediment beaches of Puget Sound, WA, USA, a large estuarine fjord. Specifically, we investigated differences in the amount of wrack, the composition of wrack, and the abundance of logs found in the upper intertidal zone of armored and unarmored beaches, as well as the role of physical factors in determining the amount and type of wrack and logs. We tested the hypotheses that (1) armored beaches are narrower, have coarser sediments, and provide less accumulation space for marine and terrestrial organic debris relative to unarmored beaches, and (2) there are qualitative differences in the types of wrack on armored and unarmored beaches due to disrupted connections between armored beaches and terrestrial environments.

Study Sites and Methods

Study sites

Puget Sound is a fjord-like estuary (Fig. 1) with large, mixed semi-diurnal tides. The tidal range at our study sites is approximately 3 m for those in central Puget Sound and 4 m in the south. The shoreline of Puget Sound is composed primarily of steep coastal bluffs of glacially derived sediments and eroding barrier beaches, with very few rocky outcrops. Most beach sediments in Puget Sound are derived from these glacial deposits and include a heterogeneous mix of clay, silt, sand and gravel; bluff erosion is the dominant mechanism that supplies these sediments to the beaches (Shipman 2010). All our study beaches had large sand and gravel sediment components. Sources of beach wrack are primarily terrestrial vegetation from the marine riparian zone, seagrass from extensive beds in the shallow subtidal zone, and algae detached from low-shore and subtidal cobbles. Salt marshes in Puget Sound have become scarce, and none of our sites were near the large river deltas containing most marsh remnants. About 1/3 of the shores of the inside waters of Washington state are armored, and the region including the City of Seattle and the islands across the sound from it is ~60% armored (Higgins et al. 2005).

Sampling occurred at 29 paired armored-unarmored beaches throughout central and south Puget Sound (Fig. 1) in spring (late April-early May) and fall (late August-early September) in 2010, 2011, and 2012, although not all sites were sampled in all years (Table 1). To examine more detailed seasonal variation in some parameters, three pairs of beaches were also sampled in winter (December) and summer (late June). Sites were initially selected from aerial shore photos, and added to the study once permission for access was acquired (most beaches in Puget Sound are privately owned). The beaches within each armored-unarmored pair were within the same drift cell (independent zone of littoral sediment transport from source to deposition area). The 29 beach pairs were in 20 different drift cells, which varied in length from 1.8 to 22.5 km. These drift cells ranged from 5-99% armored, with an average of 60%. Paired beaches were adjacent to each other or separated by up to a few hundred meters, but were always matched in terms of aspect, wave exposure, and nearshore bathymetry. Most sites were relatively open to Puget Sound's wind-waves, with fetch values of 3.0-18.6 km (sites means of 4 directions facing the Sound); sheltered inlets were not sampled, and we avoided stream and river deltas. Beach pairs were selected to represent a range of armored and natural shoreline conditions found in Puget Sound, including armoring placed at different tidal elevations (from below +2 m to above +4 m MLLW: Mean Lower Low Water), different types of armoring (e.g., concrete seawalls, riprap, retaining walls constructed of wood pilings), and different degrees of armoring in the whole drift cell. Sites were chosen without regard to backshore conditions (e.g., bank or bluff height, type of terrestrial vegetation, proximity of development) although these conditions were noted on site. A 50 meter shore-parallel transect line was selected for sampling at each beach.

Physical survey methods

Beach topography was quantified using a laser level and rod to measure elevation and distance from toe of bluff or armoring to the lowest tidal elevation possible (typically 0.0 m MLLW), as determined from water surface elevation recorded at Seattle or Tacoma stations (NOAA station ID 9447130 and 9446484). We characterized sediment grain sizes [using two different methods] at several key elevations: MLLW, MLW (Mean Low Water), the wrack line, and any other point on the foreshore where a distinct change in sediment type and slope occurred. First, in the field at three random points along the horizontal transect line we used a quadrat 32 x 32 cm (0.1 m^2) with 25 marked subdivisions to visually estimate the percent of the surface sediment in each of five size classes: Cobble (>6 cm), Pebble (4 mm to 6 cm), Granule (2-4 mm), Sand ('gritty' up to 2 mm), and Silt/Clay (smooth). Subsurface sediment (often different because of the sorting action of waves) was similarly characterized after scraping away the top 5 cm. For analyses, surface and subsurface percentages were averaged for each quadrat. [Second, sediment samples were collected as part of wrack line samples (see below) and analyzed for grain size characteristics in the laboratory.

Biological survey methods

Wrack surveys were conducted at the most recent high tide line, or at the toe of armoring in cases where armoring was present below this elevation. Our surveys did not include the older wrack often present high on unarmored shores; quantified differences in wrack between armored and unarmored shores are thus very conservative. We defined beach wrack as organic material including algal, seagrass, and terrestrial plant debris deposited on the beach. At ten random points along each transect, we used a 30 cm x 30 cm quadrat to estimate the total wrack cover (percentage of quadrat in which the sediment was covered with wrack), and the proportion of this composed of algae, eelgrass, terrestrial plant material, and human debris (trash). When possible, the types of algae were specified. For ease of visual estimation, the quadrat was divided into a 5 x 5 grid. At alternating transect points (five points total per transect), we collected wrack samples and measured logs. Wrack samples were collected using a benthic core (20 cm length x 15 cm diameter section of PVC pipe). The core was pushed down through the wrack and into the top 2.5 cm of sediment, and the contents were transferred into gallon-size Ziploc bags and brought back to the laboratory for analysis. The width of the log line was measured as the distance from the seaward-most edge of logs to the landward-most edge of the logs perpendicular to the transect point. We also counted the number of large and small logs (longer or shorter than 2 m, respectively) intersecting this perpendicular line.

Laboratory methods

To separate wrack material from the sediment in core samples, the entire sample was emptied into a pitcher and covered with 5 – 8 cm of water. The pitcher was swirled to suspend wrack material and organisms, and suspended contents poured through a 0.106 mm sieve. This process was repeated 10 times for each sample to ensure that all organisms and wrack materials were separated from the sediments.

Wrack from each sample was placed into a large plastic tray with 2 – 3 cm of tap water and sorted into categories of algae, seagrass, and terrestrial material. Primary and secondary types (by volume) of algae and terrestrial plant material were identified. Sorted wrack materials were placed in preweighed aluminum trays and dried for approximately 24 hours (or until all moisture was removed from the sample) at 60°C. Weights of dried samples were calculated to 0.001 g.

Statistical analyses

Data input into all statistical tests were per-beach mean values from the 10 (wrack cover) or 5 (log and biomass) samples per transect. Armored-unarmored differences in wrack percent cover and biomass, width and abundance of logs, and physical parameters were analyzed using paired t-tests with type (armored or unarmored) as the treatment and sites as replicates. Two-way analyses of variance (ANOVA) were used to test for differences in wrack percent cover, biomass and composition by treatment and season, and for interactions between treatment and season. Percent cover data were arcsine square-root transformed and wrack biomass data were log(X+1) transformed prior to univariate analyses to improve assumptions of normality. Composition of wrack was analyzed using multivariate techniques in PRIMER 6 to identify differences in the overall wrack assemblage and the relationship between those differences and physical predictor variables. Nonmetric multidimensional scaling (NMDS) was used to visualize relationships between samples based on Bray-Curtis similarity measures for wrack percent cover and biomass data, and Euclidean distance for environmental data, and differences among sample groups tested with PERMANOVA. Multivariate analyses were conducted on square-root transformed percent cover data, log(X+1) transformed biomass data, and normalized environmental data. The distance-based linear model (DISTLM) and distance-based redundancy analysis (dbRDA) procedure was used to link the ordination of wrack samples to physical predictor variables. All DISTLM analyses were performed step-wise using AIC selection for the fitted model.

Results

Armored and unarmored beaches within a pair clearly differed in a number of key physical parameters (Tables 1, 2). At these 29 pairs of sites, armoring of the shoreline reduced beach width (from toe of bluff or of armoring to MLW) by an average of 8.9 m, and lowered elevation of beach toe by an average of 0.9 m (up to 3.5 m in the most extreme case). These two differences were both highly significant (Table 2). Beach slope was not significantly affected by armoring at these sites, and few differences in sediment type were seen; only cobble (grains >60mm) were significantly different, with more cobbles present in the wrack line at armored beaches. When abundances of all grain sizes (including shell hash) were examined together in a multivariate analysis, a 2-factor PERMANOVA indicated that sites differed but there was no overall treatment (armoring) effect.

Overall, wrack on Puget Sound beaches was dominated by algae, especially ulvoids (*Ulva* spp. and *Ulvaria* spp., ~60% of the wrack coverage overall), a variety of red algae (9%), and *Fucus* (6%); all these commonly grow on low-shore cobbles. Eelgrass (*Zostera marina* and *Z. japonica*) was also abundant, comprising about 13% of the wrack overall, especially near sites with adjacent subtidal beds. Terrestrial detritus was about 24% of the wrack cover, consisting of diverse materials (leaves and sticks), mostly from marine riparian species such as alder trees and blackberry bushes. Wrack percent cover data from beach quadrats was clearly correlated with wrack biomass in the core samples (eelgrass cover vs. biomass $r^2 = 0.62$, algae $r^2 = 0.45$, terrestrial $r^2 = 0.23$, $N = 596$ samples), with variance stemming from these methods sampling slightly different areas, and with cover vs. mass relationships differing substantially with algal morphology and plant parts (e.g. leaves vs. sticks).

Logs in the wrack zone included both 'natural' recruits (with root wads attached) and cut logs. Many armored beaches had no drift logs at all, whereas unarmored beaches had wide log zones with both old and 'fresh' logs deposited on the high shore, and often with riparian-zone trees slumping onto the beach. The log population varied little with season; in both spring and fall, unarmored beaches had on average 16-35 times as many logs as armored beaches (Fig. 2), with the width of the log line differing correspondingly (Table 2).

The amount of wrack varied more between seasons than did the logs, with greater percent cover and biomass accumulating in the fall than in the spring (Fig. 3, Table 2). In spring there was 66% more total wrack cover on unarmored than armored beaches, and in fall the difference was 76%. The difference was particularly striking for the terrestrial component, which was 3-7 times as abundant on unarmored beaches. The composition of wrack (proportions of algae, eelgrass, and terrestrial debris) was affected by both armoring and season. The algal proportion (both percent cover and biomass) was higher at armored beaches compared to unarmored beaches, while the terrestrial proportion was higher at unarmored beaches (Table 2, Fig. 3). At the site pairs sampled in spring and fall, not only was there more total wrack in the fall but the proportion derived from algae was significantly higher at that time (Table 4, Fig. 3). The terrestrial and eelgrass proportions were correspondingly higher in spring than fall (Table 4, Fig. 3).

For the three pairs of sites with more seasonal detail (sampled in all four seasons: Table 1), the algal proportion of wrack was minimal in winter and gradually increased through the summer to the fall (Table 3, Fig. 4). Eelgrass, in contrast, was most common in winter (Fig. 4), although this difference was not significant (Table 3).

Multivariate analyses allow examination of wrack abundance and composition as a whole, and testing of the factors that affect it. Ordinations of wrack percent cover data from spring and fall both showed clear separation between armored and unarmored samples (not illustrated). Separate two-factor PERMANOVAs of spring and fall wrack data with treatment (armored/unarmored) as a fixed factor and site as a random factor (the multivariate equivalent of a paired t-test) showed that wrack 'assemblages' as a whole were significantly affected by armoring (percent covers Fall, $p = 0.001$, Spring $p = 0.002$; biomasses Fall and Spring both $p = 0.001$). A PERMANOVA of wrack percent cover data from sites sampled in all four seasons with treatment and season both as fixed factors indicated that both factors were significant, with no interaction (similar to univariate results in Table 3).

While amounts and types of wrack were clearly influenced by armoring, there was substantial site-site variation not explained by this factor. DISTLM analyses found various significant predictor variables for both wrack cover and biomass, although no combination of variables explained more than 19% of the total variation (Table 5). Variation in the composition and abundance of spring wrack cover was best explained by percent sand (with more sand associated with less wrack), percent pebble (positively associated with wrack), and maximum elevation (higher toe of bluff or armoring associated with more wrack). Variation in fall percent cover was best explained by percent cobble (with a weak negative association with wrack), percent granules (weak positive association), and maximum elevation (positive association). Variation in wrack biomass in both seasons was associated with most of the same parameters (and in the same directions), with the addition of beach slope (steeper slope weakly associated with less biomass). Sediment composition (mix of grain sizes) was best explained by maximum elevation and beach width (Table 5).

Discussion

Ecotones represent interfaces between distinct landscapes but are usually not characterized by discrete boundaries (Naiman and Decamps 1997; Polis and Hurd 1997). Shoreline armoring imposes a barrier within the gradient of the intertidal zone and thus can significantly alter ecotone dynamics at the interface between land and sea (Dugan et al. 2008; Romanuk and Levings 2003; Sobocinski et al. 2010). Our results demonstrate that armoring lowers the elevation of the marine-terrestrial transition and narrows the width of this gradient, reducing the amount of space within the marine riparian ecotone. Shoreline armoring also replaces unconsolidated pebble-sand beach sediments with immobile hard structures. Effects of these physical differences in beach structure in our study included significant loss of log accumulation in the upper shore as well as reduced abundance and altered composition of beach wrack. These changes largely reflect one of the hypothesized mechanisms of armoring impacts, "placement loss" or "encroachment" (Coyle and Dethier 2010), where covering of the upper shore with an armoring structure (often with fill behind it) simply eliminates the space where logs and wrack would normally accumulate. Our data did not document substantial effects of armoring on beach slope or sediment grain sizes, as has been shown in coastal sandy beaches, although there was slightly more cobble at our armored beaches. Beach slope and sediment changes are indicative of other armoring impacts, such as increases in wave reflection and sediment impoundment (reviewed in Coyle and Dethier 2010; Ruggiero 2010; Dugan et al. 2011). Sediments on the beaches of Puget Sound are of very mixed grain sizes and show enormous site to site variation, which appears to reflect pre-existing geological setting more than local armoring impacts (A.S. Ogston, unpubl. data).

Previous work has shown that sediment type can influence wrack deposition, with cobble beach sediments containing more wrack than sandy sediments, perhaps because more material can be trapped in the larger spaces between cobbles (Orr et al. 2005). Our DISTLM analyses indicated sediment type was a partial predictor of wrack abundance and composition, with weak trends towards more wrack with less sand and cobble but more pebbles and granules. We cannot determine if this is an indirect effect of armoring (on both grain sizes and wrack) or a direct effect of sediment porosity on ease of wrack deposition as waves carrying debris wash up the beach face.

In Puget Sound, not only does shoreline armoring decrease the overall input of debris to the upper intertidal zone, it also alters wrack composition. Wrack in the upper zone of armored beaches has about half as much biomass overall and is dominated by marine debris (algae and seagrass), which could have been derived from local or regional sources carried in by the tide. Because shoreline armoring disrupts the marine-terrestrial connection, and is often combined with removal or reduction of backshore vegetation (Romanuk and Levings 2003; Sobocinski et al. 2010), local input of organic detritus from terrestrial plants decreases at armored beaches. At our 29 pairs of beaches, backshore vegetation was much less abundant at armored than unarmored beaches (mean of 6 vs. 70 percent of the beach with overhanging vegetation, respectively), and the vegetation above armoring was often lawn rather than trees or shrubs. Higgins et al. (2005) found that across all the shores of south-central Puget Sound, trees made up 80% of the marine riparian vegetation in unarmored areas but only 46% in armored areas (where grass was more common), and the trees in armored areas rarely overhung the beach. The clear reduction in the proportion of terrestrial material in the wrack at armored beaches suggests that local backshore vegetation is the primary source of terrestrial detritus. In contrast, at unarmored beaches the wrack was composed of a mix of material from both terrestrial and marine sources.

Our study design maximized spatial replication over seasonal replication; however wrack survey results from sites sampled in all four seasons indicate that replication in spring and fall allowed us to capture much of the variation among seasons (Fig. 4). We found seasonal differences in the abundance and type of wrack, with higher overall accumulations in fall than in spring and a greater contribution of algal wrack in fall. Studies of seasonal patterns of wrack deposition on exposed sandy beaches have shown that the stranded biomass of wrack is related to periods of increased wave energy (Marsden 1991; Ochieng and Erftmeijer 1999; Barreiro et al. 2011; Gomez et al. 2012), often in fall and winter, and this also appears to be the case on our more sheltered estuarine beaches. In Puget Sound, wave energy associated with storm events is greatest in fall and winter; the algal and seagrass sources are all perennial, but greatest standing stock exists after the summer growing season and is susceptible to dislodgment in fall storms. Armored beaches have particularly low accumulations of wrack in winter and spring, even though abundant wrack was deposited at unarmored beaches during these periods. Reflection of storm waves off of armoring structures may be a mechanism inhibiting wrack accumulation there. Alternatively, wave action may transport wrack material higher on the beach profile on unarmored shores but not on armored shores because they lack upper intertidal accumulation space. Previous studies have shown that wrack abundance and composition are also influenced by beach morphology (Orr et al. 2005; Barreiro et al. 2011; Gomez et al. 2012) and our results support this. An exception to the pattern of armored beaches having lower wrack abundance was found in summer sampling (Fig. 4), when total cover was not significantly different by treatment. This result was in part due to one of the three armored beaches (24A) having a flat terrace below the seawall where high spring tides and calm wave conditions enabled large amounts of algal wrack to accumulate prior to our summer sampling date.

Shoreline armoring results in a loss of connectivity between patches landward and seaward of its location, disrupting inputs and exchange of materials, nutrients and prey resources between land and sea. Many marine nearshore foodwebs are detritus-based (Robertson and Lenanton 1984; Mann 1988; Duggins et al. 1989; Bustamante and Branch 1996; Kirkman and Kendrick 1997) and beach wrack is an important source of energy for beach consumers (Griffiths and Stenton-Dozy 1981; Polis and Hurd 1996; Dugan et al. 2003; Wright et al. 2013). Thus less wrack deposited on armored beaches results in reduced nutrient supply at the base of the food web, which likely has consequences for populations of invertebrate fauna (Lastra et al. 2008; Sobocinski et al. 2010; MacMillan and Quijón 2012). In addition, the shift on armored beaches to proportionally more marine algae and less terrestrial material changes the type of subsidy available to beach consumers. Leaf-litter and algal wrack provide both food and shelter for diverse communities of invertebrates (Colombini et al. 2000; Romanuk and Levings 2003; Abrantes and Sheaves 2008; Sakamaki and Richardson 2008; Cowles et al. 2009; Sobocinski et al. 2010); armored shorelines with reduced terrestrial organic debris thus lack the resource base to support the leaf-litter community as well as the marine debris to support algal-associated organisms. These wrack invertebrates, in turn, are exploited by larger mobile biota, e.g. birds, fish, and small mammals (Kirkman and Kendrick 1997; Rose and Polis 1998; Carlton and Hodder 2003; Dugan et al. 2003). Several studies have shown negative effects of intentional removal of wrack from beaches for aesthetic purposes, i.e. “beach grooming”, on benthic infauna and mobile consumers (Dugan et al. 2003; Gilburn 2012). Our results suggest that shoreline armoring produces a similar effect to beach grooming in terms of the amount of wrack potentially available to serve as food for beach consumers.

Armoring has a variety of local habitat impacts as well. Reduction of overhanging vegetation at armored beaches alters their microclimate, and can reduce their habitat quality, e.g. for spawning of nearshore fish (Rice 2006; Romanuk and Levings 2006). Accumulated logs are another feature that is almost entirely absent from armored beaches. Log zones serve as habitat for many organisms (Marsden 1991; Noel et al. 2005; Costall and Death 2009; Pavesi and De Mathaeis 2009; Ratcliffe and Orozco 2009), and act as natural beach stabilizers (Eamer and Walker 2010; Heathfield and Walker 2011; Nordstrom and Jackson 2012). All of our unarmored study sites had some degree of log accumulation in the supratidal, while many of our armored sites lacked logs altogether (also found by Higgins et al. 2005). Log abundance showed no variation with season, indicating that when present, logs are more permanent features of upper intertidal zones.

Subsidization of sandy, wave exposed beaches through the deposition of marine algal and seagrass wrack has been fairly well established (Polis and Hurd 1996; Dugan et al. 2003; Cowles et al. 2009; Gonçalves and Marques 2011). However, these sandy outer coast systems often lack the type of riparian zones that fringe the unarmored beaches of Puget Sound. Freshwater riparian zones subsidize the streams they border, both with organic detritus and invertebrate fauna (Mann 1988; Kawaguchi and Nakano 2001; Kawaguchi et al. 2003). There is already some evidence that marine riparian zones subsidize adjacent beaches and aquatic habitats (Marsden 1991; Romanuk and Levings 2003; Brennan and Culverwell 2004; Toft et al. 2007; Tonnes 2008; Romanuk and Levings 2010; Sobocinski et al. 2010) and our study adds to that literature, particularly with the proportion of terrestrial plant material that contributes to wrack on unarmored beaches.

The broad spatial scale, temporal replication, and paired study design are strengths of this study, and our results demonstrate clearly that armoring is more important than site, year, and season in driving differences in the amount and type of wrack and the abundance of logs on beaches. While the study occurred in Puget Sound, results are likely applicable to mixed-sediment, moderate-wave energy beaches in other parts of the world. Compared with high energy sand beaches, mixed-sediment beaches have received much less attention in the literature although they occur in many major coastal cities where negative effects of armoring are likely of ecological concern (Nordstrom 1992; Coyle and Dethier 2010). Our results add to the limited body of knowledge on the demonstrable impacts of armoring, and this knowledge has the potential to affect conservation, restoration, and management actions. From a coastal engineering perspective, there is a need for better information on the impacts and predicted responses of different shoreline stabilizing structures and practices. This can inform restoration possibilities along armored shorelines (Chapman and Underwood 2011), some of which have been implemented locally (Toft et al. 2013). From a management perspective, human well-being requires conservation of ecosystem services and creates a need for data on how current armoring practices impact ecosystem services; this should guide future best management practices (Currin et al. 2010; Nordstrom et al. 2010). In coupled human-natural systems, which exist along many coastlines worldwide, there will be little public impetus for changing current practices of shoreline development without clear understanding of impacts of armoring (Leschine 2010). Our study, and subsequent work linking wrack to food webs valued by society, should add support to the argument for changing shoreline-stabilizing practices both within Puget Sound and in other areas.

Acknowledgements

We thank Helen Berry, Jeff Gaeckle, Erin Morgan, Katie Dowell, the Wetland Ecosystem Team, and the Marine Geology Group for their assistance with field and lab work. We thank the property owners who allowed us access to their properties on the shores of Puget Sound. This research was funded in part by a grant from the Washington Sea Grant Program, University of Washington, pursuant to National Oceanic and

Atmospheric Administration Award No. R/ES-57. The views expressed herein are those of the author(s) and do not necessarily reflect the views of NOAA or any of its sub-agencies. Additional support came from the University of Washington School of Aquatic and Fishery Sciences. Matching funds were generously provided by the Washington Dept. of Natural Resources.

Table 1 Summary of study sites and sampling frequency. Seasons: spring, S; summer, Su; fall, F; winter, W. Beach width is the measured distance in meters from the armoring or bluff toe to MLW. Maximum elevation is the height in meters above MLLW. Armor type categories: vertical concrete, VC; vertical wood, VW; vertical riprap, VR; sloping riprap, SR; none, N. Supratidal vegetation categories: blackberry, BL; dunegrass, D; none, N. Backshore vegetation categories: shrubs, S; trees, T; lawn, L. Overhanging vegetation is the percent cover over the transect

Site	Sampling events		Beach width (m)	Maximum elevation (m)	Beach slope	Armor type	Bank type	Vegetation		
	Season(s)	Year(s)						Supra-tidal	Back-shore	Over-hanging
1A	S, F	2010, 2011	18.0	3.08	0.028	SR	D	BL	S	0
1U	S, F	2010, 2011	29.3	3.80	0.068	N	EB	N	T	65
2A	S, F	2010, 2011	10.9	2.17	0.120	VC	D	N	L	0
2U	S, F	2010, 2011	69.0	4.94	0.031	N	EB	BL	T	75
3A	S, F	2010	23.5	3.46	0.110	VC	VB	N	S	0
3U	S, F	2010	24.6	3.88	0.122	N	VB	BL	T	100
4A	S, F	2010	24.5	3.43	0.104	VC	VB	N	S	0
4U	S, F	2010	25.8	3.60	0.079	N	VB	BL	T	100
5A	S, F	2010	21.0	3.56	0.128	VC	D	N	L	25
5U	S, F	2010	39.5	4.18	0.084	N	VB	BL	T	100
6A	S, F	2010, 2011	23.5	3.77	0.053	VC	D	N	L	0
6U	S, F	2010, 2011	25.7	3.70	0.043	N	VB	N	T	100
7A	S, F	2010, 2011	22.5	3.76	0.129	VC	D	N	L	0
7U	S, F	2010, 2011	25.0	4.08	0.120	N	VB	N	T	65
10A	S, F	2010, 2011	20.5	3.41	0.124	VR	D	N	L	0
10U	S, F	2010, 2011	26.5	3.49	0.099	N	VB	BL	T	90
11A	S, F	2010, 2011	19.5	3.32	0.110	VW	D	N	L	0
11U	S, F	2010, 2011	27.0	3.94	0.114	N	EB	BL	T	90
12A	S, F	2010, 2011	26.4	3.07	0.067	VR	D	N	L	0
12U	S, F	2010, 2011	33.0	3.59	0.054	N	EB	BL	T	65
13A	S, Su, F, W	2010, 2011	20.0	2.86	0.100	VC	D	N	L	0
13U	S, Su, F, W	2010, 2011	27.2	4.00	0.115	N	VB	BL	T	90
14A	S, F	2011	19.5	2.67	0.072	VC	D	N	L	0
14U	S, F	2011	37.4	2.91	0.042	N	EB	N	T	65
15A	S, F	2011	25.0	3.01	0.038	VR	D	N	S	0
15U	S, F	2011	34.0	3.92	0.024	N	EB	N	T	65
16A	S, F	2011	23.0	2.59	0.068	VC	D	N	L	0
16U	S, F	2011	35.8	3.70	0.050	N	D	D	S	0
17A	S	2011	20.7	2.94	0.100	SR	VB	N	T	0
17U	S	2011	33.4	3.93	0.092	N	VB	BL	S	40
18A	S	2011	31.0	3.55	0.065	VW	D	N	L	0
18U	S	2011	41.0	3.85	0.044	N	EB	BL	S	65
19A	F	2011	19.0	2.77	0.084	VW	D	N	T	0
19U	F	2011	29.0	3.90	0.074	N	VB	BL	T	90

20A	F	2011	55.0	3.22	0.033	VW	D	N	T	15
20U	F	2011	57.0	3.86	0.033	N	VB	N	T	0
21A	F	2011	23.5	3.69	0.088	VC	VB	N	T	0
21U	S, F	2011, 2012	25.0	3.84	0.103	SR	VB	D	T	0
22A	S, F	2011, 2012	50.0	2.64	0.036	VC	D	N	L	0
22U	F	2011	50.3	4.85	0.043	N	D	D	L	0
23A	F	2011	22.0	3.16	0.071	VR	VB	N	S	65
23U	F	2011	28.5	3.53	0.080	N	EB	BL	T	65
24A	S, Su, F, W	2010, 2011	18.5	2.28	0.041	SR	D	N	L	0
24U	S, Su, F, W	2010, 2011	23.3	4.14	0.128	N	VB	D	T	100
25A	S, Su, F, W	2010, 2011	27.9	2.69	0.039	SR	D	N	L	0
25U	S, Su, F, W	2010, 2011	28.0	4.16	0.114	N	VB	BL	T	100
26A	S, F	2012	10.2	1.97	0.097	VC	D	BL	S	0
26U	S, F	2012	43.5	5.50	0.076	N	EB	BL	T	20
27A	S, F	2012	42.5	3.17	0.038	VC	D	N	L	25
27U	S, F	2012	57.5	4.74	0.042	N	VB	N	T	100
28A	S, F	2012	29.6	4.72	0.118	SR	D	N	T	35
28U	S, F	2012	24.3	5.37	0.149	N	D	D	T	75
29A	S, F	2012	23.8	3.71	0.108	VW	D	N	L	0
29U	S, F	2012	25.8	4.05	0.114	N	EB	N	T	100
30A	S, F	2012	18.7	3.50	0.137	VW	D	N	T	15
30U	S, F	2012	21.2	3.33	0.117	N	EB	BL	T	100
31A	S, F	2012	28.0	4.04	0.065	VC	D	BL	T	0
31U	S, F	2012	28.2	4.66	0.138	N	EB	N	T	100

Table 2 Summary of paired, one-way t-test results comparing armored and unarmored sample means, with pairs as replicates and type (armored vs. unarmored) as treatment (n = 29 pairs). Significant results at the α = 0.05 level are indicated by *

One-tailed, paired t-tests

	Response variable	Armored mean	Unarmored mean	p-value	summary
Physical data	Beach width (m; toe to MLW)	24.8	33.6	0.0002*	U > A
	Elevation of bluff toe or armor (m above MLLW)	3.18	4.05	< 0.0001*	U > A
	Beach slope (Toe to MLW)	0.10	0.10	0.4900	no difference
	Percent sand	40.3	38.5	0.3369	no difference
	Percent granule	8.00	8.00	0.4819	no difference
	Percent pebble	42.7	47.3	0.1584	no difference
	Percent cobble	3.15	1.03	0.0262*	A > U
Logs	Log line width (m)	0.21	5.69	< 0.0001*	U > A
	Total count of logs (average per transect point)	0.42	7.43	< 0.0001*	U > A
Percent cover	Total percent cover	19.0	32.6	< 0.0001*	U > A
	Algae percent cover	16.0	22.5	0.0168*	U > A
	Terrestrial percent cover	1.22	6.38	< 0.0001*	U > A
	Eelgrass percent cover	1.91	3.64	0.0013*	U > A
	Algae proportion of total	0.74	0.56	0.0009*	A > U
	Terrestrial proportion of total	0.16	0.31	0.0001*	U > A
	Eelgrass proportion of total	0.13	0.13	0.2140	no difference
Biomass	Average total biomass (g/sample)	1.31	2.77	< 0.0001*	U > A
	Average algae biomass (g/sample)	0.70	1.14	0.001*	U > A
	Average terrestrial biomass (g/sample)	0.36	1.31	0.0001*	U > A
	Average eelgrass biomass (g/sample)	0.20	0.29	0.1309	no difference
	Algae proportion of total biomass	0.58	0.39	0.0006*	A > U
	Terrestrial proportion of total biomass	0.29	0.51	0.0001*	U > A
	Eelgrass proportion of total biomass	0.13	0.10	0.2574	no difference

Table 3 Results (p values) of two-way ANOVAs of wrack percent cover data from intensive sites by treatment (armored = A; unarmored = U; n = 6) and season (winter, spring, summer, and fall). There were no significant interactions between type and season for any of the tests. Significant results at the α = 0.05 significance level are followed with *. Summary results are based on post-hoc Tukey's HSD tests

Two-way ANOVA, 4 seasons, intensive pairs only

Variable	Treatment	Season	Summary
Total cover	0.0143*	0.0206*	U > A, Fall > other seasons
Algae cover	0.4743	0.0009*	Fall > other seasons
Terrestrial cover	0.0002*	0.1149	U > A
Eelgrass cover	0.0009*	0.9244	U > A
Algae proportion	0.1660	<0.0001*	Winter < other seasons
Terrestrial proportion	0.0066*	0.0969	U > A
Eelgrass proportion	0.0684	0.1052	No difference

Table 4 Results (p values) of two-way ANOVAs of wrack percent cover and biomass data from site pairs sampled in spring and fall (n = 25 pairs) by treatment (armored = A; unarmored = U) and season. There were no significant interactions between type and season for any of the tests. Significant results at the α = 0.05 significance level are followed with *

2-way ANOVA: Spring-Fall, All pairs				
	Variable	Type	Season	Summary
Percent cover	Total cover	0.0003*	<0.0001*	U > A, Fall > Spring
	Algae cover	0.0798	<0.0001*	Fall > Spring
	Terrestrial cover	<0.0001*	0.1840	U > A
	Eelgrass cover	0.0052*	0.3246	U > A
	Algae proportion	0.0044*	0.0069*	A > U, Fall > Spring
	Terrestrial proportion	0.0029*	0.0271*	U > A, Spring > Fall
	Eelgrass proportion	0.6521	0.0421*	Spring > Fall
Biomass	Total biomass	<0.0001*	0.0644	U > A
	Algae biomass	0.0042*	0.0008*	U > A, Fall > Spring
	Terrestrial biomass	<0.0001*	0.7460	U > A
	Eelgrass biomass	0.2230	0.9120	no difference
	Algae proportion	0.0092*	0.0105*	A > U, Fall > Spring
	Terrestrial proportion	0.0042*	0.0277*	U > A, Spring > Fall
	Eelgrass proportion	0.6870	0.5810	no difference

Table 5 Summary of Distance-based Linear Model (DISTLM) results for wrack percent cover, wrack biomass, and sediment quadrat datasets. Best model fit predictor variables (100% of fitted model variation explained) and their individual p-values are listed, as are variables that were significant in marginal tests but not part of the fitted model. AIC and R^2 values are given for the best model fit

Dataset	Season	Fitted model predictor variables	p-value	Marginal tests	p-value	AIC	R^2
Wrack percent cover	ALL	percent sand	0.002	beach width	0.008	832.09	0.153
		percent pebble	0.001	percent cobble	0.004		
		log line width	0.006	percent granule	0.01		
		maximum elevation	0.066	percent shell hash	0.001		
	SPRING	percent sand	0.001	percent shell hash	0.031	408.89	0.19
		percent pebble	0.018				
		maximum elevation	0.089				
	FALL	percent cobble	0.008	beach slope	0.016	416.61	0.16
		percent granule	0.027	log line width	0.022		
		maximum elevation	0.016	percent shell hash	0.028		
Wrack biomass	ALL	maximum elevation	0.001	beach width	0.005	902.17	0.125
		percent sand	0.001	percent cobble	0.021		
		percent pebble	0.065	percent shell hash	0.014		
				log line width	0.004		
	SPRING	percent sand	0.002	percent pebble	0.003	468.26	0.144
		maximum elevation	0.012	log line width	0.029		
	FALL	maximum elevation	0.005	beach width	0.02	431.82	0.165
		percent sand	0.035	percent granule	0.038		
		beach slope	0.033				
Sediment quadrats	ALL	maximum elevation	0.004	beach slope	0.038	91.887	0.105
		beach width	0.085				

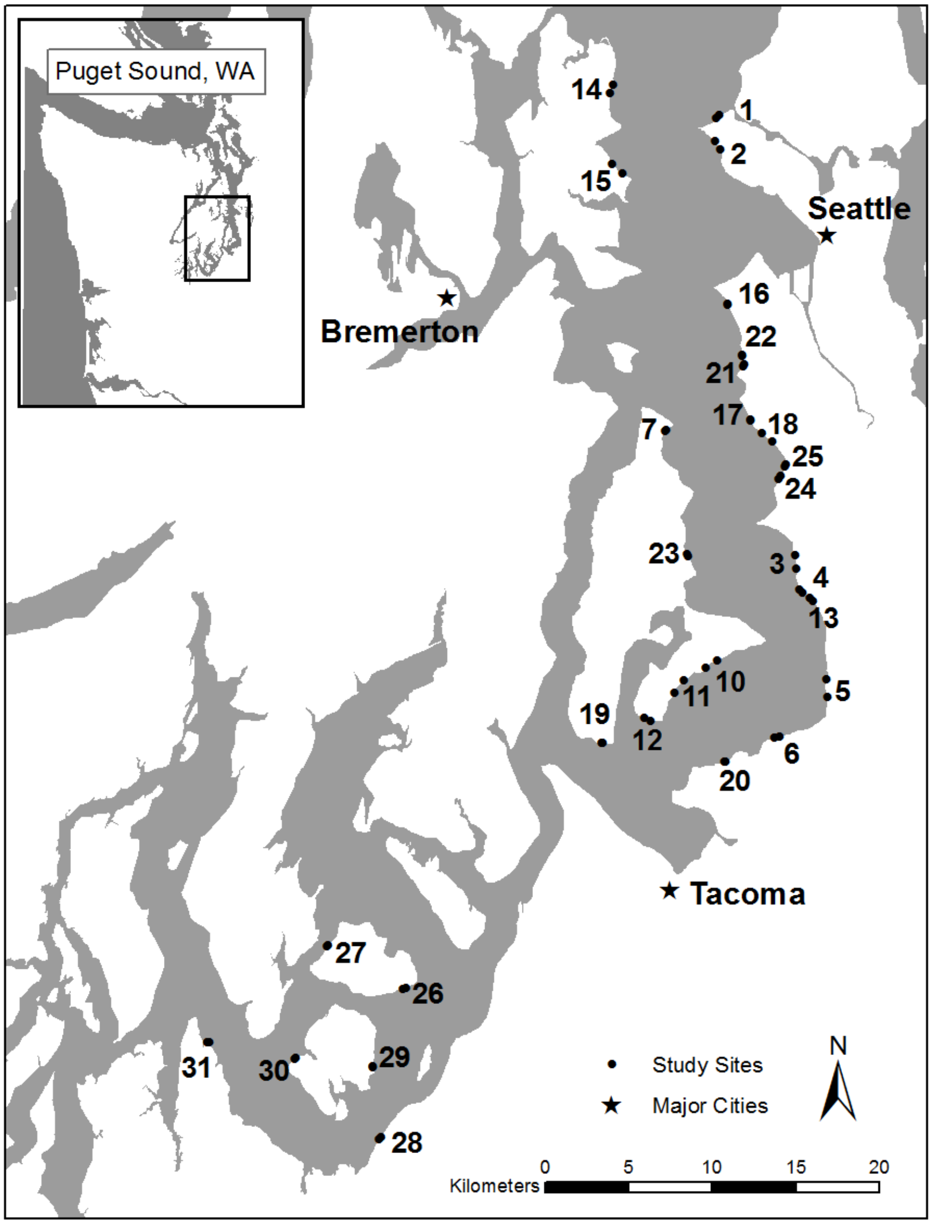

Fig. 4 Map of Puget Sound, showing study site locations and major cities. Each study beach is represented by a dot, but often the paired beaches were close enough spatially for the dots to overlap. For each site number there is an armored and an unarmored beach. Basemap data courtesy of Washington Dept. of Ecology (WA State Basemap, Place Names) http://www.ecy.wa.gov/services/gis/data.htm and Washington State Dept. of Transportation (Shoreline) http://www.wsdot.wa.gov/mapsdata/geodatacatalog/

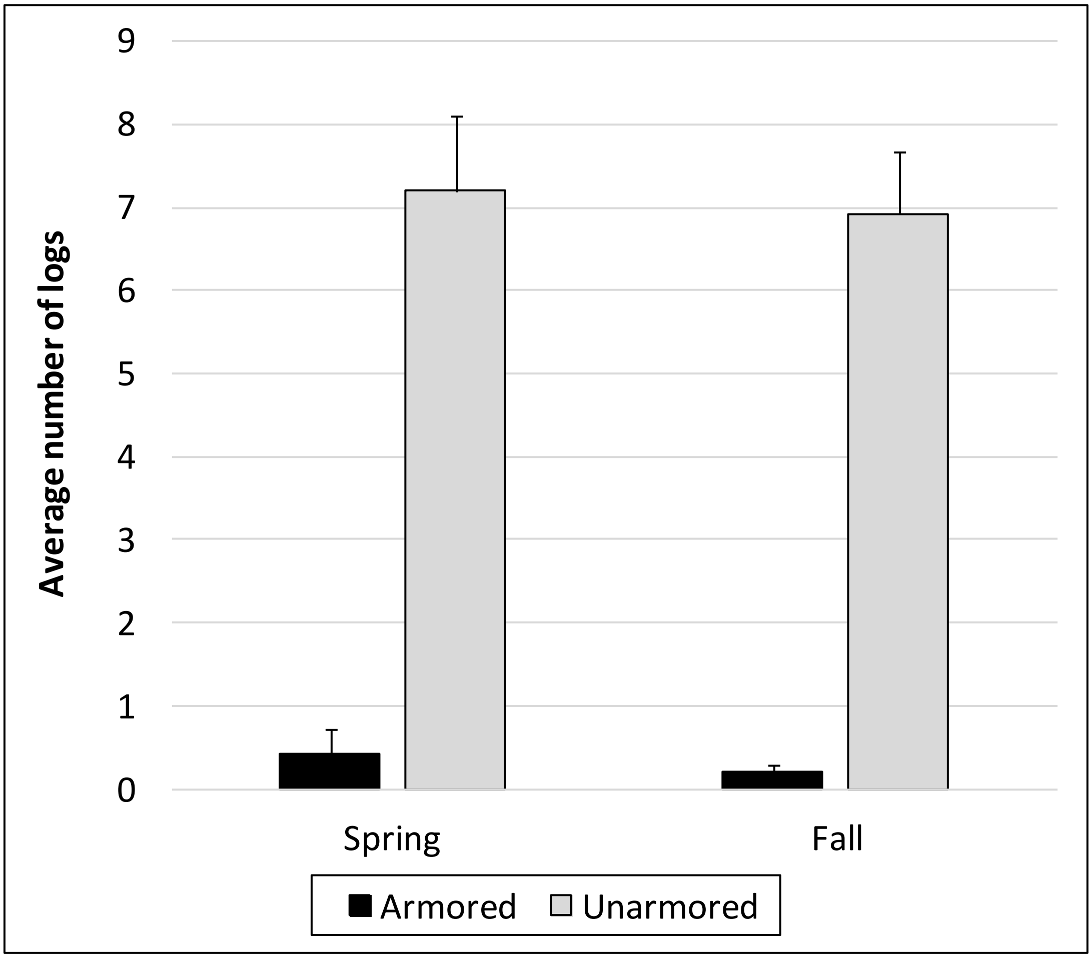

Fig. 2 Average log survey counts from armored and unarmored beaches in spring (N = 24 pairs) and fall (N = 27 pairs). Armored averages are shown in black bars and unarmored averages in grey bars. Error bars represent standard errors among the mean per-beach values

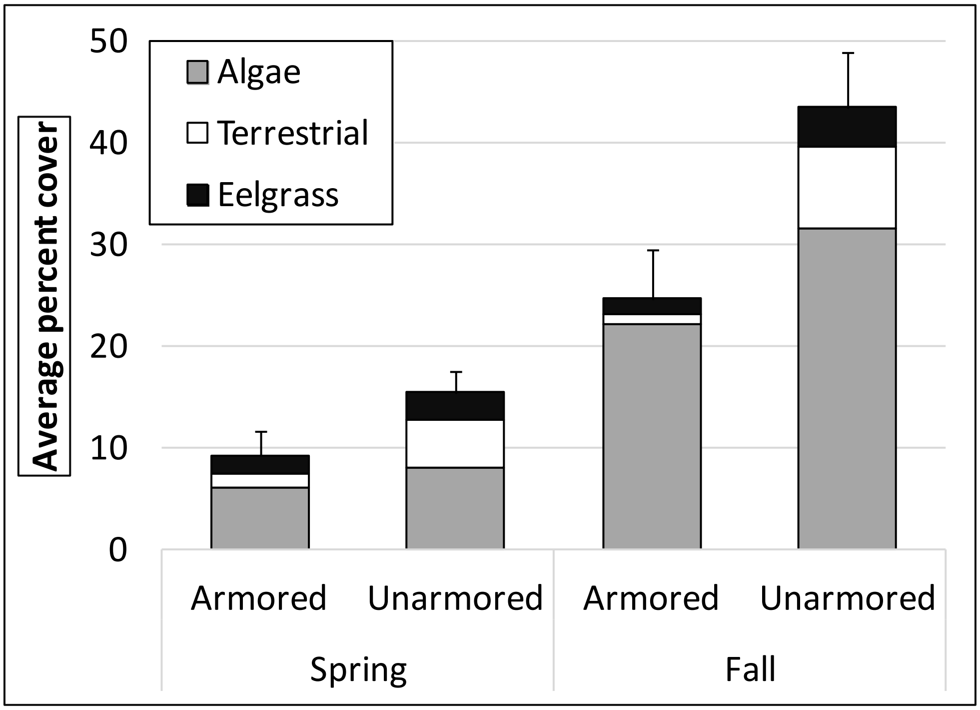

Fig. 3 Average percent cover and composition of wrack at armored and unarmored beaches in spring (N = 24 pairs) and fall (N = 27 pairs). Error bars represent standard error among the mean per-beach values

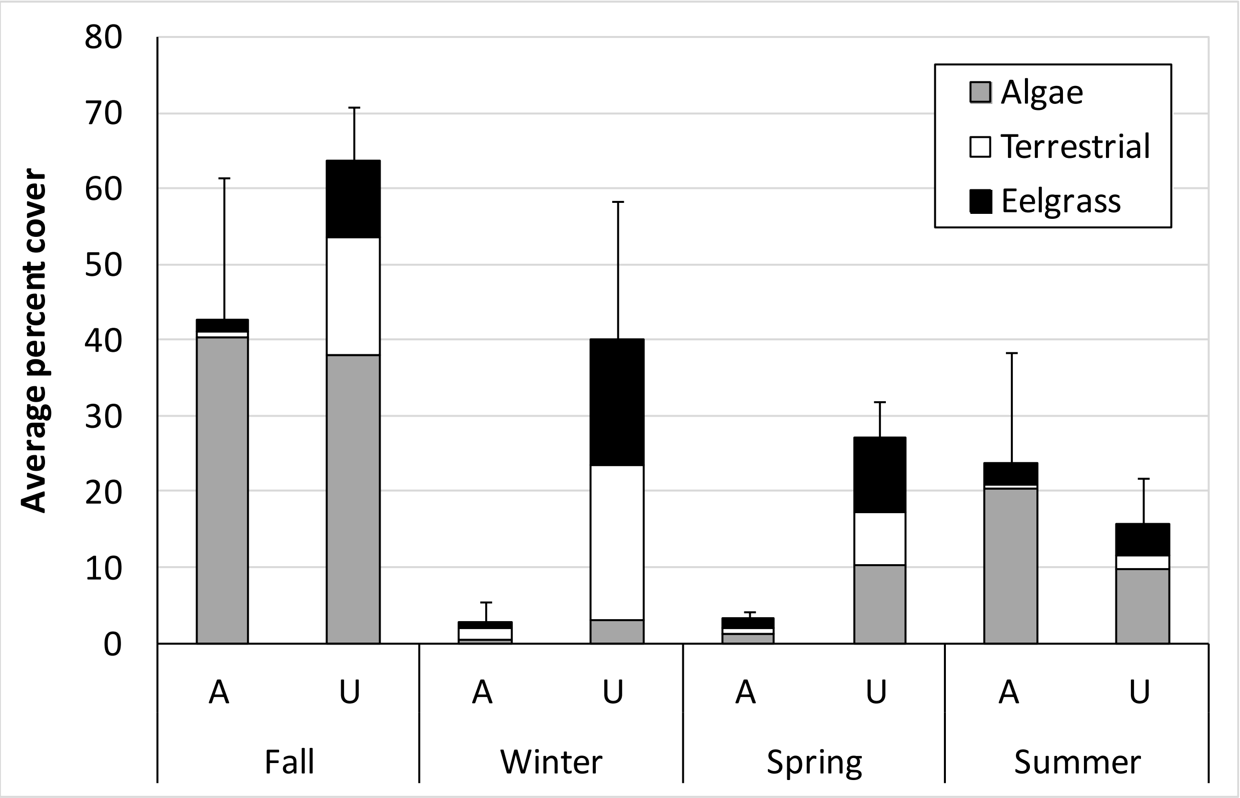

Fig. 4 Average percent cover and composition of wrack at the three armored (A) and unarmored (U) site pairs sampled in all four seasons. Error bars represent standard error among the mean per-beach values

References

Abrantes, K. and M. Sheaves. 2008. Incorporation of terrestrial wetland material into aquatic food webs in a tropical estuarine wetland. Estuarine, Coastal and Shelf Science 80: 401-412.

Barreiro, F., M. Gomez, M. Lastra, J. Lopez, and R. de la Huz. 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. Marine Ecology Progress Series 433: 65-74.

Bernatchez, P. and C. Fraser. 2012. Evolution of coastal defence structures and consequences for beach width trends, Quebec, Canada. Journal of Coastal Research 28: 1550-1566.

Brennan, J.S. and H. Culverwell. 2004. Marine riparian: an assessment of riparian functions in marine ecosystems. Washington Sea Grant, Seattle, WA, 34 p.

Brown, A. and A. McLachlan. 2002. Sandy shore ecosystems and the threats facing them: some predictions for the year 2025. Environmental Conservation 29: 62-77.

Bustamante, R. H. and G. M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196: 1–28.

Carlton, J. T. and J. Hodder. 2003. Maritime mammals: terrestrial mammals as consumers in marine intertidal communities. Marine Ecology 256: 271–286.

Chapman, M.G. 2003. Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Marine Ecology Progress Series 264: 21-29.

Chapman, M.G., and A.J. Underwood. 2011. Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. Journal of Experimental Marine Biology and Ecology 400: 302-313.

Clynick, B. G., M.G. Chapman, and A. J. Underwood. 2008. Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33: 140-150.

Colombini, I., A. Aloia, M. Fallaci, G. Pezzoli, and L. Chelazzi. 2000. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. Marine Biology 136: 531-541.

Costall, J.A. and R.G. Death. 2009. Population structure and habitat use by the spider *Latrodectus katipo* along the Manawatu-Wanganui coastline. New Zealand Journal of Zoology 36: 407-415.

Cowles, A., J.E. Hewitt, and R.B. Taylor. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. Marine Ecology Progress Series 384: 175-185.

Coyle, J.M. and Dethier, M.N. 2010. Review of shoreline armoring literature, *in* Shipman, H., Dethier, M.N., Gelfenbaum, G., Fresh, K.L., and Dinicola, R.S., eds., 2010, Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 245 – 265.

Currin, C.A., W.S. Chappell, and A. Deaton. 2010. Developing alternative shoreline armoring strategies: the living shoreline approach in North Carolina, *in* Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds. 2010. Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 91-102.

Defeo, O., A. McLachlan, D.S. Schoeman, T.A. Schlacher, J. Dugan, A. Jones, M. Lastra, and F. Scapini. 2009. Threats to sandy beach ecosystems: A review. Estuarine Coastal and Shelf Science 81: 1-12.

Duffy, E.J., D.A. Beauchamp, R.M. Sweeting, R.M., R.J. Beamish, and J.S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. T Am Fish Soc 139: 803-823.

Dugan, J. E., L. Airoldi, M.G. Chapman, S.J. Walker and T. Schlacher. 2011. Estuarine and coastal structures: environmental effects, a focus on shore and nearshore structures. Treatise on Estuarine and Coastal Science 8: 17-41.

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.

Dugan, J. E., D.M. Hubbard, I.F. Rodil, D.L. Revell, and S. Schroeter. 2008. Ecological effects of coastal armoring on sandy beaches. Marine Ecology-An Evolutionary Perspective 29: 160-170.

Duggins, D. O., C. A. Simenstad, and J. A. Estes. 1989. Magnification of secondary production by kelp detritus in coastal marine ecosystems. Science 41: 170–173.

Eamer, J. B. R. and I. J. Walker. 2010. Quantifying sand storage capacity of large woody debris on beaches using LiDAR. Geomorphology 118: 33-47.

Gilburn, A.S. 2012. Mechanical grooming and beach award status are associated with low strandline biodiversity in Scotland. Estuarine, Coastal and Shelf Science 107: 81-88.

Gomez, M., F. Barreiro, J. Lopez, M. Lastra and R. de la Huz. 2013. Deposition patterns of algal wrack species on estuarine beaches. Aquatic Botany 105: 25-33.

Gonçalves, S.C. and J.C. Marques. 2011. The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. Estuarine, Coastal and Shelf Science 95: 165-177.

Griffiths, C.L. and J. Stenton-Dozey. 1981. The fauna and rate of degradation of stranded kelp. Estuarine, Coastal and Shelf Science 12: 645-653.

Hansen, A. and F. DiCastri, eds. 1992. Landscape boundaries: consequences for biotic diversity and ecological flows. New York: Springer-Verlag.

Heathfield, D. K. and I. J. Walker. 2011. Analysis of coastal dune dynamics, shoreline position, and large woody debris at Wickaninnish Bay, Pacific Rim National Park, British Columbia. Canadian Journal of Earth Sciences 48: 1185-1198.

Higgins, K., P. Schlenger, J. Small, D. Hennessy, and J. Hall. 2005. Spatial relationships between beneficial and detrimental nearshore habitat parameters in WRIA 9 and the City of Seattle.

Proceedings of the 2005 Puget Sound Georgia Basin Research Conference. 8 pp. http://depts.washington.edu/uwconf/2005psgb/2005proceedings/papers/B7_HIGGI.pdf

Hubbard, D.M. and J.E. Dugan. 2003. Shorebird use of an exposed sandy beach in southern California. Estuarine Coastal and Shelf Science 58: 41-54.

Johnston, C.A. and R.J. Naiman. 1987. Boundary dynamics at the aquatic-terrestrial interface: the influence of beaver and geomorphology. Landscape Ecology 1: 47-57.

Kawaguchi, Y. and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology 46: 303–316.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology 84: 701–708.

Kirkman, H. and G. A. Kendrick. 1997. Ecological significance and commercial harvesting of drifting and beach-cast macro-algae and seagrasses in Australia: a review. Journal of Applied Phycology 9: 311–326.

Lastra, M., H.M. Page, J.E. Dugan, D.M. Hubbard, and I.F. Rodil. 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Marine Biology 154: 163-174.

Leschine, T.M. 2010. Human dimensions of nearshore restoration and shoreline armoring, with application to Puget Sound, *in* Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds. 2010. Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 103-113.

Levings, C. and G. Jamieson. 2001. Marine and estuarine riparian habitats and their role in coastal ecosystems, Pacific region. Canadian Science Advisory Secretariat, Research Document 2001/209, Fisheries and Oceans Canada, Ottawa, 41 p.

MacMillan, M.R. and P.A. Quijón. 2012. Wrack patches and their influence on upper-shore macrofaunal abundance in an Atlantic Canada sandy beach system. Journal of Sea Research 72: 28-37.

Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnology and Oceanography 33: 910–930.

Marsden, I.D. 1991. Kelp–sandhopper interactions on a sand beach in New Zealand. 1. Drift composition and distribution. Journal of Experimental Marine Biology and Ecology 152: 61-74.

Mellbrand, K., P.S. Lavery, G. Hyndes, and P.A. Hamback. 2011. Linking land and sea: different pathways for marine subsidies. Ecosystems 14: 732-744.

Mews, M., M. Zimmer, and D. E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328: 155–160.

Morley, S.A., J.D. Toft, and K.M. Hanson. 2012. Ecological effects of shoreline armoring on intertidal habitats of a Puget Sound urban estuary. Estuaries and Coasts 35: 774-784.

Naiman, R.J. and H. Decamps. 1997. The ecology of interfaces: riparian zones. Annual Review of Ecology, Evolution, and Systematics 28: 621-658.

Noel, L.E., S.R. Johnson, G.M. O'Doherty, and M.K. Butcher. 2005. Common eider (*Somateria mollissima* v-*nigrum*) nest cover and depredation on central Alaskan Beaufort Sea barrier islands. Arctic 58: 129-136.

Nordstrom, K.F. 1992. Estuarine Beaches. London: Elsevier Science Publishers, 224 p.

Nordstrom, K. F. and N. L. Jackson. 2012. Physical processes and landforms on beaches in short fetch environments in estuaries, small lakes and reservoirs: A review. Earth Science Reviews 111: 232-247.

Nordstrom, K.F., N.L. Jackson, and P. Rafferty. 2010. Mitigating the effects of bulkheads on the Bay Shore Island National Seashore, *in* Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds. 2010. Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 57-65.

Ochieng, C.A. and P.L.A. Erftemeijer. 1999. Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. Aquatic Botany 65: 221–238.

Orr, M., M. Zimmer, D.E. Jelinski, M. Mews. 2005. Wrack deposition on different beach types: Spatial and temporal variation in the pattern of subsidy. Ecology 86: 1496-1507

Pavesi, L. and E. De Matthaeis. 2009. Life history of the talitrid amphipod *Macarorchestia remyi* (Schellenberg, 1950) on a Tyrrhenian sandy beach, Italy. Hydrobiologia 635: 171-180.

Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28: 289–316.

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.

Quinn, T., K. Krueger, K. Pierce, D. Penttila, K. Perry, T. Hicks and D. Lowry. 2012. Patterns of surf smelt, Hypomesus pretiosus, intertidal spawning habitat use in Puget Sound, Washington state. Estuaries and Coasts 35: 1214-1228.

Ratcliffe, B.C. and J. Orozco. 2009. A review of the biology of *Pericoptus truncatus* (Fabr.) (Coleoptera: Scarabaeidae: Pentodontini) from New Zealand and a revised description of the third instar. Coleopterists Bulletin 63: 445-451.

Rice, C.A. 2006. Effects of shoreline modification on a northern Puget Sound beach: microclimate and embryo mortality in surf smelt (Hypomesus pretiosus). Estuaries and Coasts 29: 63-71.

Robertson, A.I. and R.C.J. Lenanton. 1984. Fish community structure and food-chain dynamics in the surf-zone of sandy beaches - the role of detached macrophyte detritus. Journal of Experimental Marine Biology and Ecology 84: 265-283.

Robertson, A.I. and J.S. Lucas. 1983. Food choice, feeding rates, and the turnover of macrophyte biomass by a surf-zone inhabiting amphipod. Journal of Experimental Marine Biology and Ecology 72: 99-124.

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.

Romanuk, T.N. and C D. Levings. 2006. Relationships between fish and supralittoral vegetation in nearshore marine habitats. Aquatic Conservation – Marine and Freshwater Ecosystems 16: 115-132.

Romanuk, T.N. and C.D. Levings. 2010. Reciprocal subsidies and food web pathways leading to Chum salmon fry in a temperate marine-terrestrial ecotone. Plos One 5: e10073.

Rose, M.D. and G.A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. Ecology 79: 998–1007.

Ruggiero, P. 2010. Impacts of shoreline armoring on sediment dynamics *in* Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds. 2010. Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 179-186.

Sakamaki, T. and J.S. Richardson. 2008. Retention, breakdown, and biological utilisation of deciduous tree leaves in an estuarine tidal flat of southwestern British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 65: 38-46.

Shipman, H. 2010. The geomorphic setting of Puget Sound: implications for shoreline erosion and the impacts of erosion control structures, *in* Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds. 2010. Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 19-34.

Schlacher, T.A., J.E. Dugan, D.S. Shoeman, M. Lastra, A. Jones, F. Scapini, and A. McLachlan. 2007. Sandy beaches at the brink. Diversity and Distributions 13: 556-560.

Sobocinski, K.L., J.R. Cordell and C.A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuaries and Coasts 33: 699-711.

Tabor, R. A., K.L. Fresh, R.M. Piaskowski, H.A. Gearns, and D. B. Hayes. 2011. Habitat use by juvenile Chinook salmon in the nearshore areas of Lake Washington: effects of depth, lakeshore development, substrate, and vegetation. North American Journal of Fisheries Management 31: 700-713.

Toft, J.D., J.R. Cordell, C.A. Simenstad, and L.A. Stamatiou. 2007. Fish distribution, abundance, and behavior along city shoreline types in Puget Sound. North American Journal of Fisheries Management 27: 465-480.

Toft, J.D., A.S. Ogston, S.M. Heerhartz, J.R. Cordell, and E.E. Flemer. 2013. Ecological response and physical stability of habitat enhancements along an urban armored shoreline. Ecological Engineering 57: 97-108.

Tonkin, S.P., T. Abbe, J. Carrasquero, and S. Morrison. 2007. Field measurements of shore conditions to assess bulkhead effects in Thurston County, South Puget Sound. Coastal Sediments ’07: Proceedings of the Sixth International Symposium on Coastal Engineering and Science of Coastal Sediment Processes.

Tonnes, D.M. 2008. Ecological functions of marine riparian areas and driftwood along North Puget Sound shorelines. M.S. Thesis, University of Washington.

Wright, A.N., J. Piovia-Scott, D.A. Spiller, G. Takimoto, L.H. Yang and T.W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos 122: 1496-1504.

Zimmer, M., S.C. Pennings, T.L. Buck, and T.H. Carefoot. 2004. Salt marsh litter and detritivores: a closer look at redundancy. Estuaries 27: 753–769.

Chapter 3: Shoreline armoring in an estuary alters community composition and reduces the abundance of wrack-associated invertebrates in the nearshore ecotone

Authors

Sarah Heerhartz, Jason Toft, Jeffery Cordell, Andrea Ogston, Megan Dethier

Abstract

Beach wrack is an organic subsidy that supports supralittoral invertebrate communities in many coastal systems. When beaches are fringed with riparian vegetation, wrack is sourced from both marine and terrestrial ecosystems in the form of detached macroalgae and seagrass and terrestrial leaf litter. Previous research has shown that shoreline armoring disrupts marine-terrestrial connectivity and alters the amount and composition of beach wrack. We sampled invertebrates associated with beach wrack at 29 paired armored and unarmored beaches in central and south Puget Sound, WA. Invertebrate assemblages were significantly different between armored and unarmored beaches. Unarmored invertebrate assemblages were characterized by talitrid amphipods and adult and larval dipteran and coleopteran insects (flies and beetles) and correlated with the amount of beach wrack and logs, the proportion of terrestrial material in wrack, and the maximum elevation of the beach.

Introduction

Ecotones are interfaces, or transition zones, between two distinct adjacent ecosystems. As the interface between land and sea, the marine-terrestrial (henceforth, nearshore) ecotone converges on the intertidal zone, where an exchange of organic materials occurs in the form of beach wrack: piles of seaweed, seagrass, and terrestrial plant debris suspended in water and deposited on shore as the tide ebbs. Beach wrack is an organic subsidy, consisting of material that crosses ecosystem boundaries and becomes available to consumers from both systems. Beach wrack supports primary consumers (Dugan et al. 2003; Ince et al. 2007; Cowles et al. 2009; MacMillan and Quijón 2012), which in turn are consumed by organisms from both aquatic and terrestrial ecosystems (Hubbard and Dugan 2003; Stapp and Polis 2003; Lewis et al. 2007; Wright et al. 2013), either by direct foraging in the wrack zone or by consuming prey transported to the adjacent ecosystem. Wrack plays an important role in shaping beach invertebrate communities (Colombini et al. 2000; Cowles et al 2009; MacMillan and Quijón 2012), and wrack-associated invertebrates are key players in nutrient cycling and decomposition (Griffiths and Stenton-Dozey 1981; Mews et al. 2006; Lastra et al. 2008). Where beaches are fringed with riparian vegetation, wrack may be composed of both aquatic and terrestrial components, representing a reciprocal subsidy. Shoreline armoring, defined as artificial shore-hardening structures that are intended to prevent coastal erosion, disrupts nearshore ecotone linkages (Romanuk and Levings 2003; Toft et al. 2010) and alters the amount and type of wrack and logs deposited and retained on the upper shore (Higgins et al. 2005; Tonnes 2008; Sobocinski et al. 2010; Heerhartz et al. in revision). Thus disrupted connectivity likely has consequences not only for primary consumers that depend on wrack and logs for food and shelter, but also for secondary consumers that are subsidized by resources from the adjacent ecosystem, for example juvenile salmon (*Oncorhynchus* spp.) that forage on terrestrial insects.

In open coast sandy beach ecosystems, armoring results in narrowing and artificial hardening of the beach (placement loss; Defeo et al. 2009; Bernatchez and Fraser 2012) and alteration of invertebrate communities (Dugan et al. 2008; Sobocinski et al. 2010). Estuarine beaches fringed with riparian vegetation and composed of coarse gravel substrates, like those found in Puget Sound, differ ecologically from open-coast sandy beaches but their response to armoring has received less attention in the literature. Overall reduction in the amount of wrack on armored shores (Tonnes 2008; Sobocinski et al. 2010) and differences in the proportions of marine and terrestrial material (Romanuk and Levings 2003; Heerhartz, et al., in revision) likely affects upper intertidal invertebrate communities, particularly talitrid amphipods and wrack-associated flies and beetles. Other studies have found positive relationships between the amount of wrack and the abundance of supralittoral invertebrates (Ochieng and Erfmeijer 1999; Dugan et al. 2003; MacMillan and Quijón 2012) and shown that, within wrack invertebrate communities, different species may utilize and/or consume different types of wrack material (Colombini et al. 2000; Pennings et al. 2000; Ince et al. 2007). We investigated the role of wrack in shaping upper intertidal invertebrate communities and armoring-related differences, specifically: assemblages of talitrid amphipods and insects within beach wrack, the type and abundance of mobile invertebrates across the upper intertidal zone at armored and unarmored beaches, and the role of detritivorous talitrid amphipods and insects in wrack decomposition.

Our objective was to quantify the effects of armoring on supralittoral invertebrate assemblage composition and dynamics in estuarine nearshore environments. We tested the following hypotheses: (1) unarmored beaches have higher abundances of wrack-associated and marine riparian invertebrates and different upper intertidal invertebrate assemblages compared to armored beaches; (2) wrack decomposition rate is directly related to abundances of macroinvertebrates, and is thus slower at armored beaches than unarmored beaches; and, (3) mobile invertebrate abundance and composition differs by tidal elevation and armored-unarmored differences are most apparent at upper elevations where armoring is placed.

Methods

Study sites

We sampled 29 paired armored-unarmored beaches in south and central Puget Sound, a fjord-like estuary in Washington State (Fig. 1). Sampling occurred in spring (late April-early May) and fall (late August-early September) from 2010 to 2012, although not all sites were sampled in all years or by all sampling methods (Table 1). Puget Sound is characterized by mixed semi-diurnal tides, which increase in magnitude from north to south, and range at our study sites from approximately 3 m in central Puget Sound to 4 m in the south. The primary sediment composition at our study sites is a mix of sand and gravel derived from glacial deposits and predominantly delivered to beaches from episodic bluff erosion and distributed by longshore transport within drift cells (Shipman 2010). Beach pairs were initially selected from aerial shore photos to encompass a range of armored and natural shoreline conditions found in Puget

Sound, including armoring at different tidal elevations (from below +2 m to above +4 m MLLW: Mean Lower Low Water), different types of armoring (e.g., concrete seawalls, riprap, retaining walls constructed of wood pilings), and different degrees of armoring of the whole drift cell. Paired beaches were matched in terms of aspect, wave exposure, and nearshore bathymetry and were adjacent in most cases; mean distance between transects was 383 m, maximum distance was 1 km.

Wrack and macroinvertebrate composition

We sampled invertebrates associated with wrack and underlying sediment at all beach pairs in the spring and fall. We surveyed wrack along a 50-m transect at each beach corresponding with the line of most recent wrack deposition, and logs were surveyed at whatever tidal elevation they were found. Armored beaches that lacked wrack and logs were surveyed at the highest tidal elevation possible, in natural beach substrates at the toe of armoring. Percent cover and composition of wrack were measured in ten randomly spaced 0.9-m^2 quadrats along each transect. Samples of wrack and the top 2.5 cm of sediment were collected using a 15-cm diameter benthic corer at five of the quadrat points. The number of small and large logs was counted and the width of the log line perpendicular to shore measured at the same five points where wrack was collected. Wrack samples were brought back to the lab and frozen until processing. Following thawing, we sorted the wrack into seagrass, algae, and marine debris, dried it for 24 hours (or until all moisture was removed) at 60° C, and weighed each component to quantify the percent composition and biomass, and identified and counted all invertebrates with the aid of a dissecting microscope. Talitrid amphipods and other crustaceans were identified to genus level, other invertebrates were identified to family level (except oligochaetes, which were not identified beyond Class).

Sediment grain sizes at the wrack line were characterized at each beach. At three random points along the horizontal transect line we used a quadrat 32 x 32 cm (0.1 m^2) with 25 marked subdivisions and visually estimated the percent of the surface sediment in each of five size classes: Cobble (>6 cm), Pebble (4 mm to 6 cm), Granule (2-4 mm), Sand (‘gritty’ up to 2 mm), and Silt/Clay (smooth). Subsurface sediment (often different because of the sorting action of waves) was similarly characterized after scraping away the top 5 cm. For analyses, surface and subsurface percentages were averaged for each quadrat.

Wrack decomposition and associated invertebrates

We measured wrack decomposition rates in the presence or absence of invertebrate macrofauna at selected beaches in 2010 and 2011 (Table 1) using experimental containers full of dried, weighed beach wrack. Five pairs of wrack-filled PVC tubes were anchored onto the surface of the sediment at random locations along a 50-m transect in the upper intertidal (either along the highest wrack line or at the base of armoring) and left out for approximately 30 days. Pairs consisted of two 15-cm long x 5-cm diameter tubes, one with ends covered with fine (130-µm) mesh to exclude talitrid amphipods and one with coarse mesh (5-mm) to allow talitrids and other macroinvertebrates to enter. The tubes were filled with 6 g (+/- 0.05 g) of clean, dry wrack consisting of a mix of algae, seagrass, and leaves in 2010 and equal parts ulvoids (*Ulva* spp.) and eelgrass (*Zostera marina*) in 2011. The difference between the initial dry weight of wrack and the final dry weight remaining in each tube upon collection was used to estimate decomposition rates. All invertebrates present in the tubes upon collection were brought back to the laboratory and identified as above.

Mobile invertebrates at different beach elevations

To quantify the composition, abundance and activity of mobile invertebrates along upper and lower wrack lines simultaneously at armored and unarmored beaches, we deployed pitfall traps consisting of 473-ml (16-oz) plastic cups filled with ~3 cm of filtered seawater mixed with a small amount of biodegradable soap to break the surface tension at all study sites in 2011 and 2012. We noticed that unarmored beaches often had two wrack lines, one corresponding with the recent higher high tide, and one lower on the shore (with smaller amounts of wrack) corresponding with an approximate tidal elevation of 2.44 m (+8 ft) MLLW. Armored beaches often lacked the higher wrack line, but within each pair the low wrack line was usually present at both beaches. We used pitfall traps to address the questions of: (1) whether invertebrate assemblages differ between the higher and lower wrack lines, and (2) whether invertebrate abundance and taxa composition at low wrack lines are more similar between armored and unarmored beaches than the upper wrack lines. Five traps were placed at random along two 50-m transects (10 traps total): one along the high wrack line and the second along the low wrack line (exact elevations of these were variable and were visually located based on wrack deposits on each sampling event). Trap contents were collected after one hour, preserved in 7% buffered formalin, and taken back to the laboratory, where invertebrates were identified to species level (talitrid amphipods, to determine whether species composition differed by elevation) or family level (insects) whenever possible and counted with the aid of a dissecting microscope.

Statistical analysis

We tested for differences in mean abundances of key invertebrate taxa groups from armored-unarmored beach pairs with paired t-tests using means per beach, and treating sites as paired replicates. We used two-way analysis of variance (ANOVA) to test for differences in mean invertebrate abundances in pitfall traps by shore type and elevation, and in wrack tubes by shore type and mesh size. Differences in wrack decomposition in tubes were analyzed by mesh size and year using two-way ANOVA. Relationships between wrack tube invertebrate abundances and decomposition were tested using linear regression. We used permutational multivariate analysis of variance (PERMANOVA; PRIMER v6 with PERMANOVA+; Clarke and Gorley 2006; Anderson et al. 2008) to test for differences in invertebrate assemblages in wrack samples and pitfall traps between armored and unarmored beaches (type as fixed factor) with sites as replicates (pair as random factor). Relationships between environmental predictor variables and wrack sample invertebrate assemblages were investigated using distance-based linear modeling (DISTLM) and distance-based redundancy analysis (dbRDA). The DISTLM procedure was conducted using the step-wise selection procedure to maximize the Akaike information criterion (AIC). These analyses partition the multivariate variability of the invertebrate assemblages along best-fit axes and then test the environmental variables that are most closely related to these axes.

A log(X+1) transformation was applied to invertebrate abundance data prior to parametric testing to reduce right skewness, and prior to multivariate analyses to reduce the contribution of abundant species relative to rare species in resemblance matrices. Proportions of wrack decomposed in tubes were binomially distributed so we applied an arcsine square root transformation to improve normality. Resemblance matrices for multivariate tests of invertebrate abundances were based on Bray-Curtis similarity. Prior to DISTLM and dbRDA analysis, we removed any inter-correlated physical predictor variables (criterion $R^2 \geq 0.55$) and rare invertebrate taxa (contributing less than 5% to overall abundances).

Results

Wrack and macroinvertebrate composition

Invertebrate taxa groups tested showed significant differences between armored and unarmored beaches (Fig. 2). There were significantly more talitrid amphipods (one-tailed test, $p < 0.0001$), more insects (one-tailed test, $p = 0.002$), and fewer aquatic invertebrates (one-tailed test, $p = 0.01$) at unarmored sites compared to armored sites (Fig. 2). Talitrid abundances were most strikingly different, with unarmored beaches having on average 8.5 times more than at armored beaches. Differences in overall wrack invertebrate assemblages existed regardless of season; taxonomic composition and abundances of invertebrates were significantly different between armored and unarmored beaches in both fall (PERMANOVA $p = 0.001$) and spring ($p = 0.002$).

Invertebrate assemblage composition was significantly related to a diverse set of environmental variables in both spring and fall (Fig. 3). The fitted DISTLM models explained 42% of the total variation in wrack invertebrate assemblage using six environmental predictor variables for spring samples, and 39% of the total variation using eight predictor variables for fall samples (Table 2). The particular variables showed different degrees of importance with season, but in each case invertebrate assemblages were correlated with some sediment variables (e.g., % cover granules), the amount of wrack (e.g. algal biomass), the type of wrack (e.g. proportion of wrack biomass made of eelgrass blades), and beach characteristics (e.g. elevation of the toe of bluff or of armoring). As many of these variables correlate with armoring, e.g. width of the log zone and amount of terrestrial wrack, these analyses suggest some of the mechanisms responsible for the armored/unarmored differences in invertebrates. These relationships likely result from a combination of factors including food sources (amount and type of wrack) and physiological requirements of the organisms (e.g. sediment moisture and temperature maintained by logs and wrack).

Wrack decomposition and associated invertebrates

Tubes containing wrack and left on the beach for 30 days were colonized by significantly different invertebrate assemblages at armored and unarmored beaches. Tubes at armored beaches contained significantly fewer of all invertebrate taxa except nematodes and aquatic invertebrates, with over eight times as many total invertebrates in tubes at unarmored sites (Two-way ANOVA, $p < 0.0001$). Mesh size also strongly affected colonizing invertebrate assemblages; there were significantly more talitrid amphipods, insects, collembolans, and total invertebrates in tubes with coarse mesh (Two-way ANOVA, $p = 0.001$, 0.001, 0.0002, $p < 0.0001$, respectively). Oligochaetes and arachnids (mostly small mites) showed no difference with mesh size, and nematodes were more abundant in fine mesh tubes than coarse mesh tubes ($p < 0.0001$).

Many (54 of 128) of the tubes emplaced below armoring were lost, destroyed, or empty after 30 days, whereas 105 of 128 unarmored tubes were recovered intact. Thus we could not determine whether the decomposition seen in the remaining tubes at the armored sites was related to invertebrate activity, to longer periods of submergence due to their lower elevation, or to mechanical action from tubes bumping against armoring structures. Since we wanted to determine the role of invertebrates in wrack decomposition, we only calculated decomposition rates for tubes at unarmored sites, which remained mostly dry and undisturbed during deployment. The effects of mesh size and year on decomposition were calculated from unarmored sites only. Wrack decomposed significantly faster in coarse-mesh tubes (Fig. 4; p <

0.00004). There was no significant effect of year ($p = 0.16$) and no interaction between mesh size and year. We compared per-tube relationships between the invertebrates present after 30 days and the proportion of wrack decomposed; decomposition was positively related to densities of talitridae ($R^2 = 0.204$, $p < 0.00002$) and oligochaetes ($R^2 = 0.203$, $p < 0.00002$). No other taxa groups showed any relationship to the proportion of decomposed wrack.

Mobile invertebrates at different beach elevations

Pitfall traps, which sampled invertebrates actively moving around the upper shore at low tide, showed no differences between the average number of invertebrates caught per trap higher vs. lower in the wrack zone, but substantial differences at armored vs. unarmored beaches (Fig. 5; 2-factor ANOVA; type $p = 0.03$, height $p = 0.219$). Talitrid amphipods were significantly more abundant in unarmored samples, with no difference between high and low samples (type $p = 0.0005$, height $p = 0.54$). Average insect abundances were significantly affected by type ($p = 0.003$) and elevation ($p = 0.03$), with more insects in unarmored compared to armored sites, and more insects in samples along high compared to low wrack lines. Average collembolan abundances did not vary with either factor.

Because our high and low wrack line samples were balanced and overall abundances did not differ by elevation, we pooled pitfall trap invertebrates across elevations for PERMANOVA to examine whole-assemblage differences between armored and unarmored beaches. Differences in overall pitfall trap invertebrate assemblages between armored and unarmored beaches were significant (PERMANOVA $p = 0.005$).

Discussion

In the nearshore ecotone, connectivity between marine and terrestrial ecosystems influences the amount and type of organic material deposited on the upper shore (Romanuk and Levings 2003; Heerhartz, et al., in revision), which in turn affect macroinvertebrate communities that use wrack and logs as habitat. Shoreline armoring disrupts this connectivity, reduces the total amount and the terrestrial proportion of organic material delivered to the upper shore (Tonnes 2008; Coyle and Dethier 2010; Sobocinski et al. 2010; Heerhartz et al., in revision), and results in significantly different invertebrate assemblages, including substantially fewer wrack-associated and marine riparian invertebrates in the supralittoral zone. Similar results have been found both for sandy beaches (Dugan et al. 2008) and for estuarine coastlines (Romanuk and Levings 2003; Tonnes 2008; Sobocinski et al. 2010), and the high degree of spatial replication in our study adds strong evidence that this is a widespread impact of shoreline armoring in many coastal ecosystems. One major mechanism by which shoreline armoring alters supralittoral invertebrate assemblages is by preventing beach wrack and logs from accumulating along the upper shore by encroaching on upper intertidal accumulation space. Wrack and logs provide habitat for many organisms, including talitrid amphipods, isopods, and insects (Bustamante and Branch 1996; Colombini et al 2000; Dugan et al. 2003; Costall and Death 2009). Beach wrack also provides food for these invertebrates, which in turn provide food for secondary consumers both landward and seaward of the wrack zone, such as fish (Romanuk and Levings 2010), birds (Dugan et al. 2003), crabs (Lewis et al. 2007), lizards (Barrett et all. 2005; Wright et al. 2013), and rodents (Stapp and Polis 2003).

While many studies have established the importance of marine macroalgae and seagrasses as subsidies to sandy beach ecosystems and adjacent terrestrial ecosystems (Bustamante and Branch 1996; Polis and Hurd 1996; Gonçalves and Marques 2011; Mellbrand et al. 2011), few have examined the role of a reciprocal subsidy from the land to the beach. Reciprocal subsidization may be minimal in many marine open coast systems, but in estuarine systems fringed with riparian vegetation there can be an exchange of nutrients, detritus and prey items from terrestrial and aquatic ecosystems in both directions across the ecotone (Romanuk and Levings 2003, 2010; Heerhartz et al., in revision). Such reciprocal subsidization focused in the ecotone between aquatic and terrestrial ecosystems occurs between freshwater streams and adjacent riparian ecosystems (Nakano and Murakami 2001; Baxter et al. 2005). We suggest that it is also important in estuarine nearshore ecotones like those in Puget Sound (Heerhartz et al. in revision). Our analyses showed that predictor variables explaining variation in invertebrate assemblage composition and abundance included both terrestrial factors (including biomass and proportion of terrestrial wrack, and the width of the log line) and aquatic materials (biomass of algae and proportion of eelgrass material in beach wrack). In general, terrestrial material and maximum elevation of the beach were positively associated with invertebrate assemblage composition at unarmored beaches, particularly with talitrids, dipterans, and coleopterans. These results add strong evidence for the importance of terrestrial inputs to nearshore ecosystems that include riparian vegetation. The mechanisms of disruption caused by shoreline armoring include placement loss when armoring covers the upper beach (lower maximum toe elevation), and loss of the terrestrial component in the wrack (Heerhartz et al. in press).

Invertebrates living in beach wrack are in turn likely to be a subsidy to consumers in adjacent ecosystems. Insects such as dipterans (flies) carried by wind onto the water surface provide food for juvenile salmon in shallow nearshore waters. Songbirds from riparian habitats forage in beach wrack and feed on talitrid amphipods found there (Chapter 5). All of our study methods and results point to the same conclusion of significantly different invertebrate assemblages, including fewer important prey taxa (talitrids, insects) along armored shorelines. Previous research has shown that armored shorelines accumulate significantly less wrack and logs compared with unarmored shorelines. We provide evidence that reduced wrack result in significantly different, and typically less taxa rich and abundant, invertebrate communities. In nearshore estuarine ecosystems where a substantial amount of shoreline is armored, the disruption of this ecotone may have a detrimental effect on secondary consumers that rely on beach wrack invertebrates for food.

Our pitfall traps captured fewer talitrid amphipods and insects/collembolans at armored beaches, and showed overall assemblage differences between armored and unarmored beaches. Previous studies have shown spatial differences in inter- and intraspecific distributions of talitrid amphipods (Aimee et al. 2011), but we did not detect any differences in either species or age (juvenile or adult) between high and low pitfall traps. Recently, Mantzouki et al. (2012)

showed that pitfall traps effectively measure talitrid amphipod abundance but not cohort composition. The lack of differences found between high and low wrack samples may have been due to the small distance between them (approximately 1.2 m vertical and 2 m horizontal distance depending on beach slope), the lack of sampling lower on the shore, or the short duration of sampling (1 hour). Despite the low wrack line samples being placed at the same elevation on both armored and unarmored beaches, there was a significant difference in invertebrate abundances, indicating that the effects of armoring for some organisms extend below the immediate structure.

Wrack line invertebrates play an important ecosystem role not only as prey for other organisms, but as decomposers of the abundant wrack that accumulates on estuarine beaches as well as open coasts (Griffiths and Stenton-Dozey 1981; Mews et al. 2006; Lastra et al. 2008). Our decomposition experiments provided data on the components of the invertebrate assemblage that would be essential to this process. The invertebrates present at the end of the experiment indicated that the different mesh sizes achieved the purpose of excluding (in the case of fine mesh) or allowing (in the case of coarse mesh) macroinvertebrate access to the wrack contained within the tubes. Nematodes were unexpectedly abundant in fine mesh tubes compared to coarse mesh tubes, possibly due to the exclusion of potential predators or competitors for food or space. Despite their high abundances in the fine mesh tubes, nematodes showed no correlation with decomposition rates. Talitrid amphipods and oligochaetes, however, were strongly positively correlated with decomposition rates. A caveat to this result is that we quantified the final proportion of wrack lost and the number of organisms present at the time of collection. Previous studies have indicated that macroinvertebrate colonization of wrack on sandy beaches varies through time with wrack age (Colombini et al. 2009; Pelletier et al. 2011). Quantifying both invertebrates and decomposition at progressive time intervals throughout the study duration would provide a better understanding of the role of macroinvertebrates in wrack decomposition.

In Chapter 2 (Heerhartz et al. in press) we found that shoreline armoring reduces the abundance of wrack and logs available for food and habitat in the upper intertidal and alters the composition of wrack, armored beaches having proportionally more marine (particularly algae) and less terrestrial material compared to unarmored beaches. Invertebrate assemblages reflected this difference with fewer wrack-associated and marine riparian invertebrates and more aquatic invertebrates in wrack samples and fewer invertebrates actively moving around upper intertidal substrates as quantified in the pitfall traps. Our study corroborates results for invertebrates found in a previous study of effects of shoreline armoring on Puget Sound beaches (Sobocinski et al. 2010); our approach of sampling multiple pairs of armored-unarmored beaches expands the scale of inference. We were able to control for variability in environmental parameters, ensuring our ability to test for armoring related differences. By all sampling methods, we came to the conclusion that talitrid amphipods and insects are greatly reduced in response to armoring. These groups of invertebrates provide food for many other organisms, linking beach wrack subsidies to higher trophic levels within and across the terrestrial-marine/estuarine ecotone. Their lower abundances at armored beaches suggests a mechanism by which shoreline armoring might cascade to organisms occupying higher trophic levels and impact nearshore food webs.

Table 1 Summary of sampling periods and methods conducted at each beach pair (see numbers in Fig. 1) in each of the three years of study. Bold numbers in brackets show the total number of pairs sampled.

	Wrack samples	Wrack tubes	Pitfall traps
Fall 2010	1-7, 10-12, 24, 25 **[12]**	1, 2, 6, 10, 12, 13, 24 **[7]**	-
Spring 2011	1, 2, 6, 10-18, 24, 25 **[14]**	1, 2, 6, 10, 13, 24 **[6]**	-
Fall 2011	6, 7, 10, 14-16, 19-23 **[11]**	-	6, 7, 10, 14-16, 19-23 **[11]**
Spring 2012	21, 22, 26-31 **[7]**	-	6, 13, 16, 21, 22, 24-31 **[12]**
Fall 2012	26-31 **[6]**	-	26-31 **[6]**

Table 2 Results of sequential tests in distance based linear model (DistLM) analyses for fall and spring wrack invertebrates. Variables are defined as follows: Granule, percent of sediment in quadrats categorized as granule; EelProp, proportion of eelgrass biomass in wrack; LogWidth,

measured width of log zone in upper intertidal; TerrProp, proportion of terrestrial material biomass in wrack; Algae, dry biomass of algal wrack material; MaxElev, elevation of the toe of armoring or bluff; Terrestrial, dry biomass of terrestrial wrack material; BeachSlope, average beach slope from toe of armor or bluff to mean low water.

Season	Number of variables selected	Variable	AIC	p-value	Cumulative variation explained	Residual DF
Spring	6	Granule	334.6	0.004	0.10758	42
		EelProp	332.43	0.003	0.18818	41
		LogWidth	331.22	0.013	0.24528	40
		TerrProp	330.11	0.019	0.29673	39
		Algae	326.38	0.002	0.38272	38
		MaxElev	325.81	0.034	0.41774	37
Fall	8	MaxElev	444.93	0.001	0.1182	58
		TerrProp	442.86	0.002	0.17602	57
		Terrestrial	441.35	0.004	0.22277	56
		Granule	440.02	0.012	0.26474	55
		Algae	438.51	0.005	0.30655	54
		EelProp	437.66	0.028	0.3387	53
		LogWidth	437.12	0.044	0.36616	52
		BeachSlope	437.11	0.118	0.38702	51

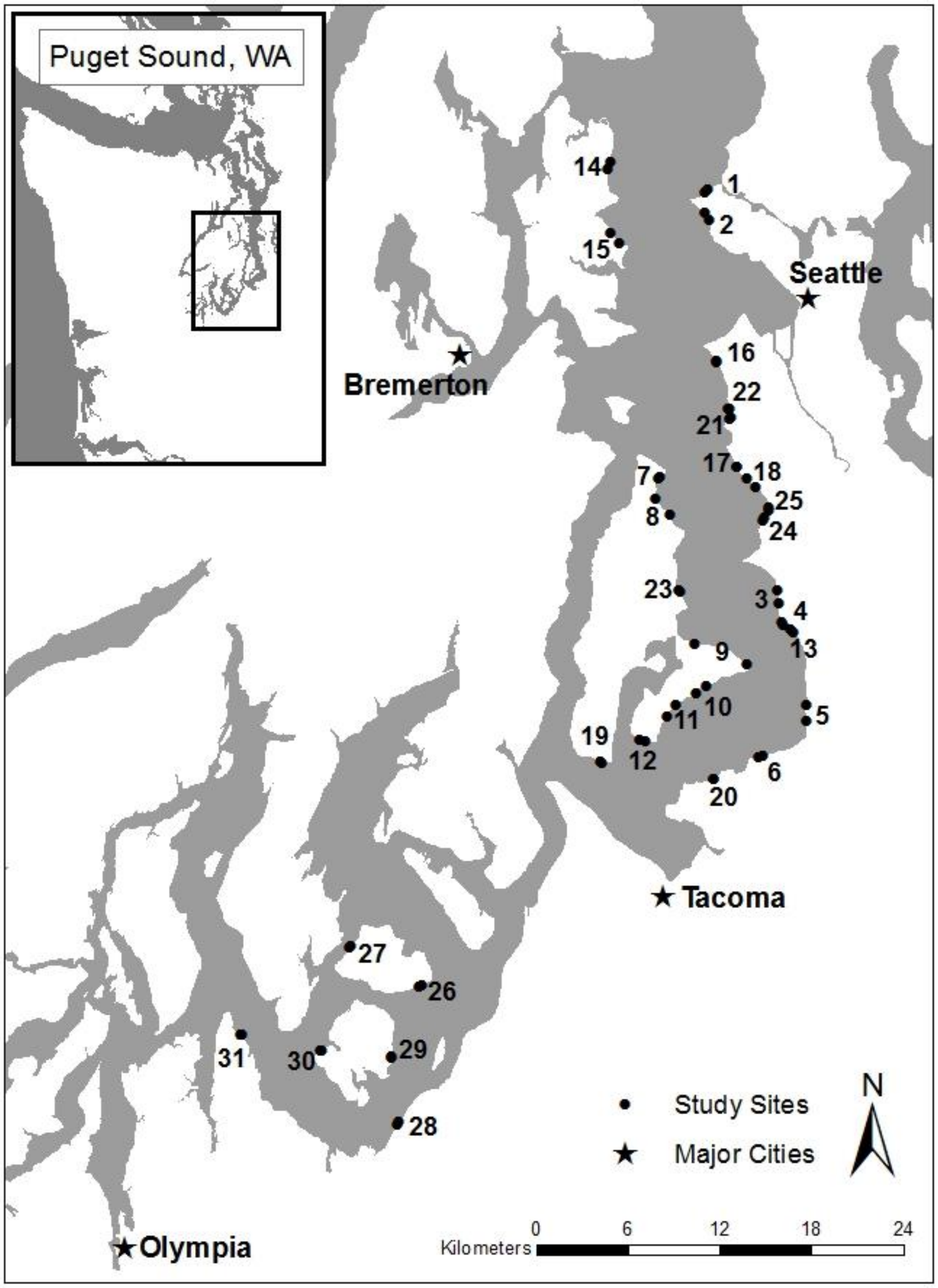

Figure 1 Map of Puget Sound, showing study site locations and major cities. Each study beach is represented by a dot, but often the paired beaches were close enough spatially for the dots to overlap. For each site number there is an armored and an unarmored beach. Basemap data courtesy of Washington Dept. of Ecology (WA State Basemap, Place Names) http://www.ecy.wa.gov/services/gis/data.htm and Washington State Dept. of Transportation (Shoreline) http://www.wsdot.wa.gov/mapsdata/geodatacatalog/

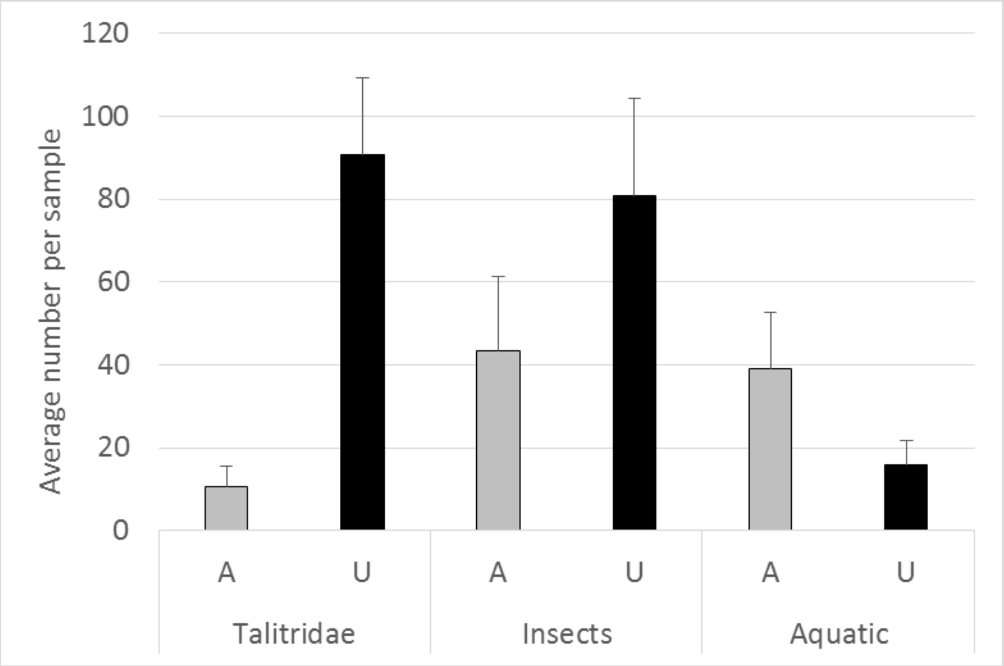

Figure 2 Summary of average invertebrate abundances from wrack samples. Armored (A) means are shown in gray, unarmored (U) means shown in black. Error bars represent standard error of the mean. Differences in armored and unarmored means were statistically significant for all taxa groups shown here.

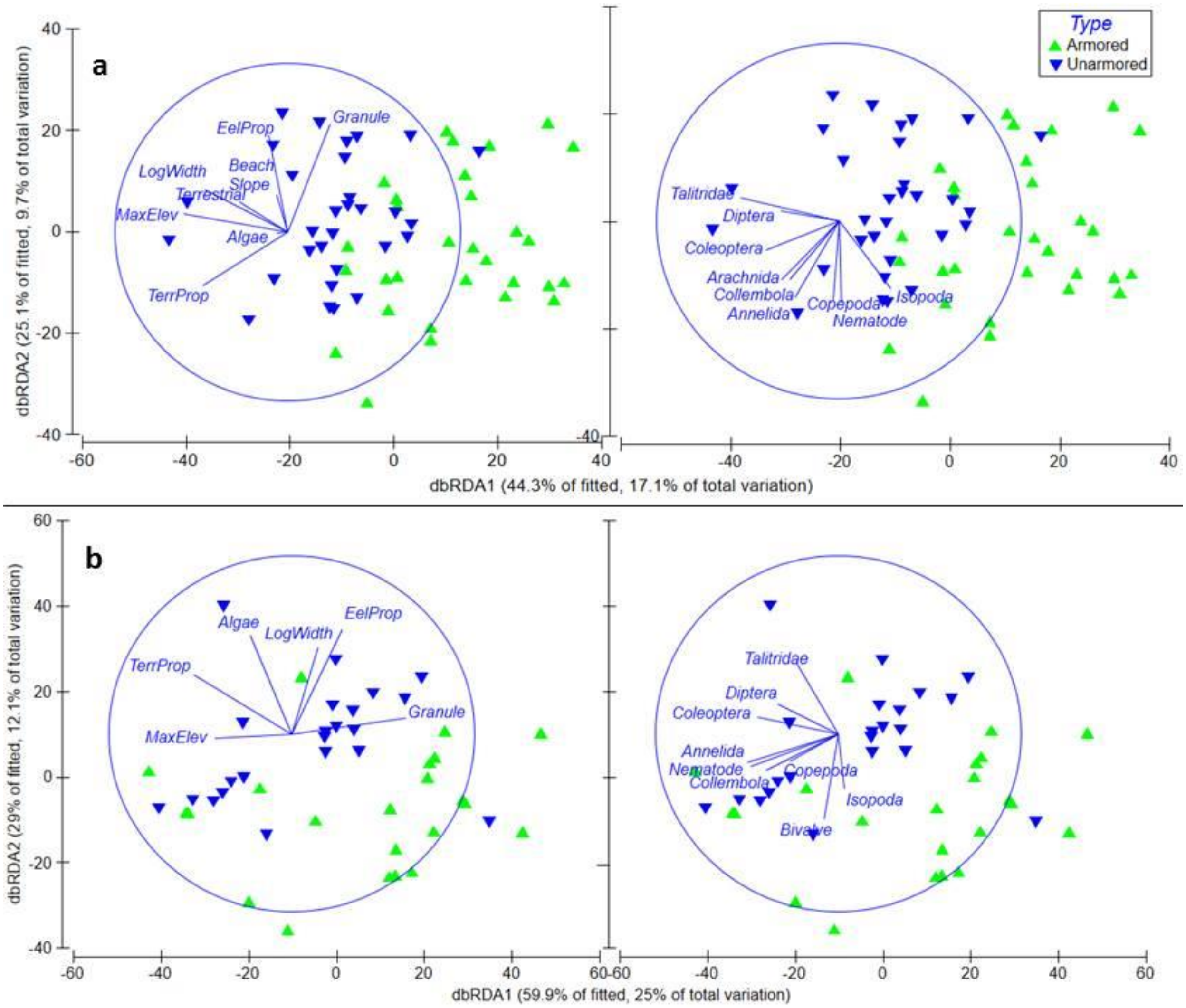

Figure 3 Distance-based redundancy analysis (dbRDA) plots of fall (a) and spring (b) wrack invertebrate samples, with rare taxa excluded. Data points represent the average invertebrate abundances for a single beach, and points are plotted with respect to one another based on Bray-Curtis similarity. The left plot shows the physical predictor variables from the wrack line (defined in Table 2); longer vectors indicate stronger relationships between the variables and the variation along the dbRDA axes. The right plot shows the invertebrate taxa most closely related to the axes.

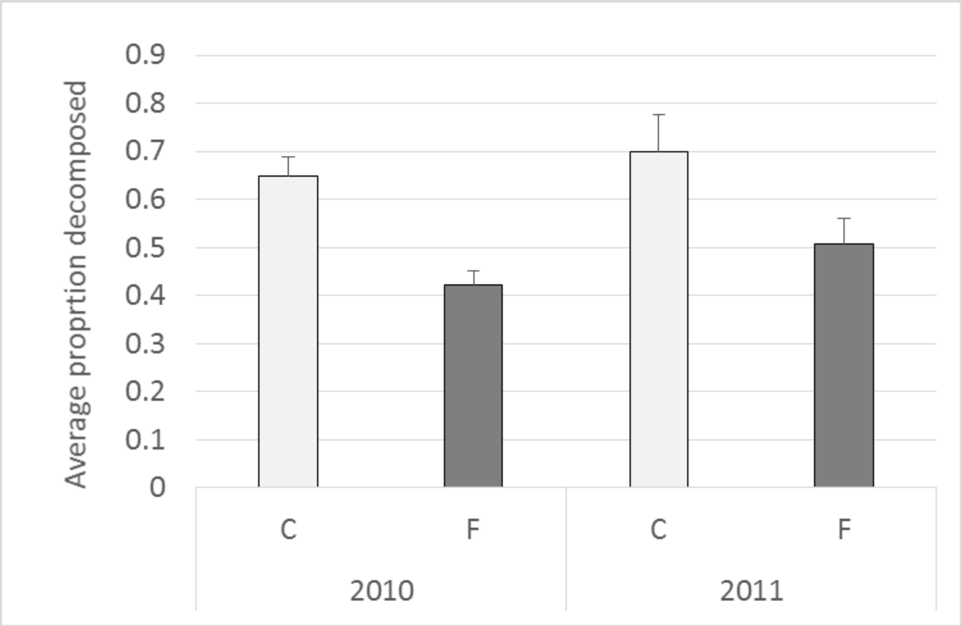

Figure 4 Average decomposition of wrack in tubes by year and mesh size (coarse, C, light gray; fine, F, dark gray). Sample sizes are N = 28, 28, 18, and 23, respectively. Error bars represent standard error of the mean.

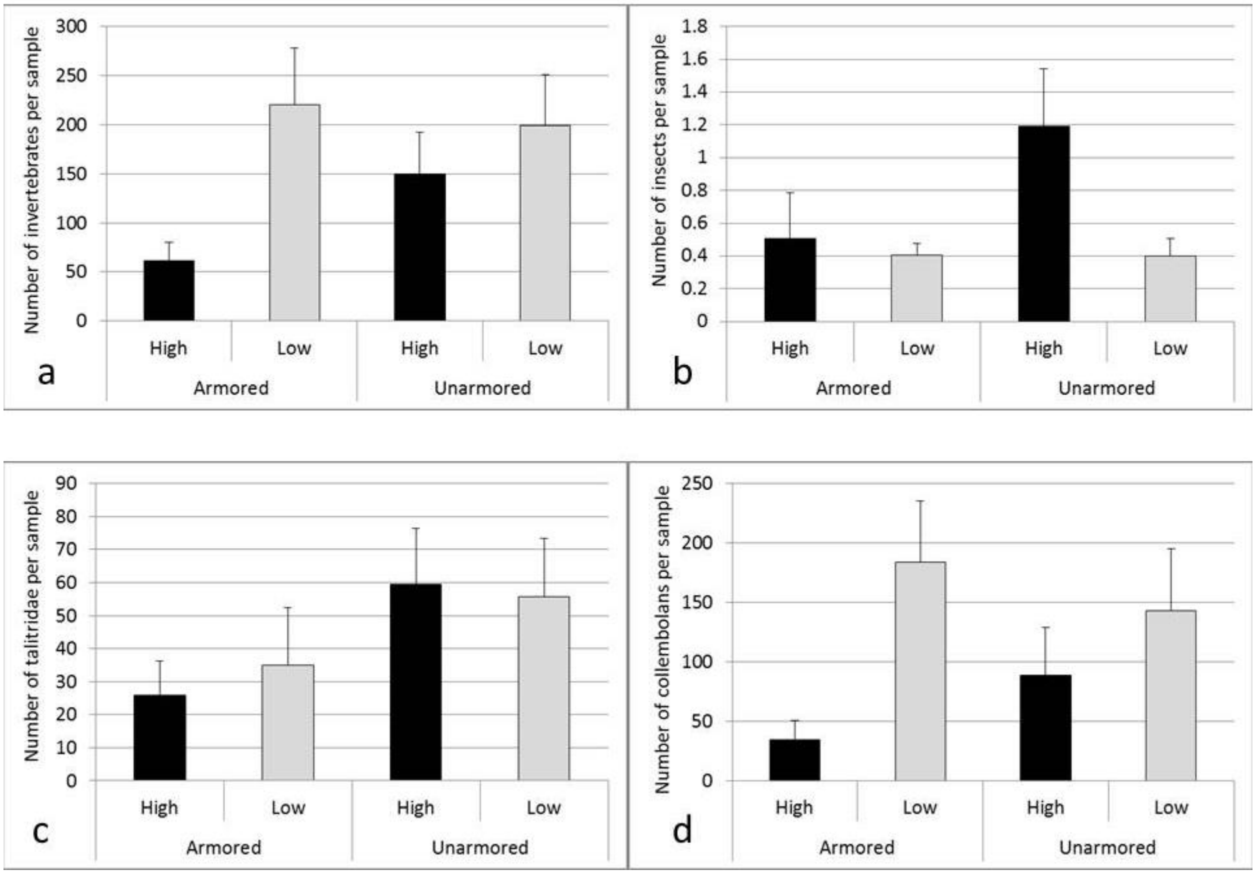

Figure 5 Average invertebrate counts per pitfall trap sample: a) total invertebrates; b) insects; c) talitridae; d) collembola. Within each plot, armored means are the two leftmost bars and unarmored means are the two rightmost bars. Means from high wrack line samples (labeled "High") are shown in black bars; means from low wrack line samples (labeled "Low") are shown in gray bars. Error bars represent standard error of the mean, N = 30 for each bar.

References

Anderson, M.J., R.N. Gorley, and K.R. Clarke. 2008. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E: Plymouth, UK.

Barrett, K., W.B. Anderson, D.A. Wait, L.L. Grismer, G.A. Polis, and M.D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations Oikos 109: 145-153.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Bernatchez, P. and C. Fraser. 2012. Evolution of coastal defence structures and consequences for beach width trends, Quebec, Canada. Journal of Coastal Research 28: 1550-1566.

Bustamante, R. H. and G. M. Branch. 1996. The dependence of intertidal consumers on kelp-derived organic matter on the west coast of South Africa. Journal of Experimental Marine Biology and Ecology 196: 1–28.

Clarke, K.R. and R.N. Gorley. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
Colombini, I., A. Aloia, M. Fallaci, G. Pezzoli, and L. Chelazzi. 2000. Temporal and spatial use of stranded wrack by the macrofauna of a tropical sandy beach. Marine Biology 136: 531-541.

Colombini, I., M.A. Mateo, O. Serrano, M. Fallaci, E. Gagnarli, L. Serrano, and L. Chelazzi. 2009. On the role of *Posidonia oceanica* beach wrack for macroinvertebrates of a Tyrrhenian sandy shore. Acta Oecologica 35: 32–44.

Cowles, A., J.E. Hewitt, and R.B. Taylor. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. Marine Ecology Progress Series 384: 175-185.

Costall, J.A. and R.G. Death. 2009. Population structure and habitat use by the spider *Latrodectus katipo* along the Manawatu-Wanganui coastline. New Zealand Journal of Zoology 36: 407-415.

Defeo, O., A. McLachlan, D.S. Schoeman, T.A. Schlacher, J. Dugan, A. Jones, M. Lastra, and F. Scapini. 2009. Threats to sandy beach ecosystems: A review. Estuarine Coastal and Shelf Science 81: 1-12.

Duarte, C., E. Jaramillo, H. Contreras, and K. Acuna. 2010. Cannibalism and food availability in the talitrid amphipod *Orchestoidea tuberculata*. Journal of Sea Research 64: 417-421.

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.

Dugan, J. E., D.M. Hubbard, I.F. Rodil, D.L. Revell, and S. Schroeter. 2008. Ecological effects of coastal armoring on sandy beaches. Marine Ecology-An Evolutionary Perspective 29: 160-170.

Gonçalves, S.C. and J.C. Marques. 2011. The effects of season and wrack subsidy on the community functioning of exposed sandy beaches. Estuarine, Coastal and Shelf Science 95: 165-177.

Griffiths, C.L. and J. Stenton-Dozey. 1981. The fauna and rate of degradation of stranded kelp. Estuarine, Coastal and Shelf Science 12: 645-653.

Higgins, K., P. Schlenger, J. Small, D. Hennessy, and J. Hall. 2005. Spatial relationships between beneficial and detrimental nearshore habitat parameters in WRIA 9 and the City of Seattle. Proceedings of the 2005 Puget Sound Georgia Basin Research Conference. 8 pp. http://depts.washington.edu/uwconf/2005psgb/2005proceedings/papers/B7_HIGGI.pdf

Ince, R., G.A. Hyndes, P.S. Lavery, and M.A. Vanderklift. 2007. Marine macrophytes directly enhance abundances of sandy beach fauna through provision of food and habitat. Estuarine Coastal and Shelf Science 74: 77-86.

Lewis, T.L., M. Mews, D.E. Jelinski, and M. Zimmer. 2007. Detrital subsidy to the supratidal zone provides feeding habitat for intertidal crabs. Estuaries and Coasts 30: 451-458.

MacMillan, M.R. and P.A. Quijón. 2012. Wrack patches and their influence on upper-shore macrofaunal abundance in an Atlantic Canada sandy beach system. Journal of Sea Research 72: 28-37.

Mantzouki, E., F. Ysnel, A. Carpentier, and J. Pétillon. 2012. Accuracy of pitfall traps for monitoring populations of the amphipod *Orchestia gammarella* (Pallas 1766) in saltmarshes. Estuarine, Coastal and Shelf Science 113: 314-316.

Mews, M., M. Zimmer, and D.E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328: 155–160.

Mellbrand, K., P.S. Lavery, G. Hyndes, and P.A. Hamback. 2011. Linking land and sea: different pathways for marine subsidies. Ecosystems 14: 732-744.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98: 166-170.

Ochieng, C.A. and P.L.A. Erftemeijer. 1999. Accumulation of seagrass beach cast along the Kenyan coast: a quantitative assessment. Aquatic Botany 65: 221–238.

Olabarria, C., M. Incera, J. Garridoa, I. Rodil, and F. Rossi. 2009. Intraspecific diet shift in *Talitrus saltator* inhabiting exposed sandy beaches. Estuarine, Coastal and Shelf Science 84: 282–288.

Pelletier, A.J.D., D.E. Jelinski, M. Treplin, and M. Zimmer. 2011. Colonisation of beach-cast macrophyte wrack patches by Talitrid amphipods: a primer. Estuaries and Coasts 34:863–871.

Pennings, S.C., T.H. Carefoot, M. Zimmer, J.P. Danko, A. Ziegler. 2000. Feeding preferences of supralittoral isopods and amphipods Canadian Journal of Zoology 78: 1918-1929.

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.

Romanuk, T.N. and C.D. Levings. 2010. Reciprocal subsidies and food web pathways leading to Chum salmon fry in a temperate marine-terrestrial ecotone. Plos One 5: e10073.

Sobocinski, K.L., J.R. Cordell and C.A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuaries and Coasts 33: 699-711.

Stapp, P. and G.A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134: 496-504.

Tonnes, D.M. 2008. Ecological functions of marine riparian areas and driftwood along north Puget Sound shorelines. MS Thesis, University of Washington, School of Marine and Environmental Affairs.

Wright, A.N., J. Piovia-Scott, D.A. Spiller, G. Takimoto, L.H. Yang and T.W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos 122: 1496-1504.

Chapter 4: Movement patterns and feeding behavior of juvenile salmon (*Oncorhynchus* spp.) along armored and unarmored estuarine shorelines

Sarah M. Heerhartz and Jason D. Toft

School of Aquatic and Fishery Sciences
University of Washington
Box 355020, Seattle, WA 98195

Corresponding author: S. M. Heerhartz
Email: sarmarie@uw.edu
Tele: 001 206 948 7206
Fax: 001 206 685 7471

Abstract

Estuarine nearshore environments are important habitats for many organisms, including juveniles of several Pacific salmon species (*Oncorhynchus* spp.). These habitats provide shallow water and high prey productivity, but are increasingly modified by anthropogenic activity including shoreline armoring, which disrupts connectivity between aquatic and terrestrial realms and artificially steepens the shore. Such effects may have adverse consequences for juvenile salmon, particularly Chinook (*O. tshawytscha*) and chum (*O. nerka*), which are known to rely on shallow, productive nearshore habitats for foraging and refuge from predators during their outmigration from natal streams to the sea. We developed snorkel methods to quantify feeding rates, movement rates, and path complexity of juvenile salmon along armored and unarmored shorelines in Puget Sound, WA, USA. We found that juvenile salmon had relatively high feeding rates along all shoreline types, but that path straightness and movement rates showed some variation between armored and unarmored sites. Feeding fish swam in more complex paths and were observed in larger schools than non-feeding fish, and path straightness and movement rate were negatively correlated with proportion of time feeding. Feeding behavior, school size, and movement rates also showed variation by species. Shoreline type (armored or unarmored) influenced juvenile salmon distribution, and unarmored shorelines appear to accommodate a greater diversity of movement patterns than armored shorelines. Our results show that juvenile salmon feed at high rates along armored and unarmored estuarine shorelines, thus decreased prey availability or altered prey resources are likely the most detrimental effects of armoring in estuarine nearshore ecosystems.

Keywords: juvenile salmon, shoreline armoring, snorkel survey, feeding rates, estuarine nearshore, movement rates

Introduction

Estuarine habitats are often highly productive foraging zones for juvenile salmon (*Oncorhynchus* spp.) (Healey 1982; Simenstad et al. 1982; Thorpe 1994), providing them with transitional habitats for physiological adjustment before they move into higher-salinity nearshore waters. Estuarine residence can be a time of rapid growth for juvenile salmon prior to marine entry (Duffy et al. 2005; Simmons et al. 2013), and growth during estuarine residence has been shown to positively influence marine survival (Duffy and Beauchamp 2011). In the spring and summer, estuaries often support high densities and diversities of insects, benthic and planktonic crustaceans and other invertebrates that are preyed upon by juvenile salmon; this high productivity coupled with high consumption rates contributes to rapid growth in these habitats (Wissmar and Simenstad 1988; Koehler et al. 2006; Duffy et al. 2010).

In many parts of their range, juvenile salmon spend some of their early lives in habitats that have been altered by anthropogenic modification and may experience multiple stressors as they migrate and feed (Loge et al. 2005), including water pollution (Stein et al 1995; Johnson et al. 2007a; Johnson et al. 2007b), loss of habitat space (McClure et al. 2008; Schaffer et al. 2009), and reduced prey production (Romanuk and Levings 2003; Sobocinski et al. 2010). Shoreline armoring – hard structures such as seawalls or riprap bulkheads built to prevent coastal erosion – can constitute a stressor for outmigrating juvenile salmon using nearshore habitats for foraging, physiological transition, and refuge from predators. One known effect of shoreline armoring is reduced aquatic-terrestrial connectivity resulting in decreased inputs of high-energy insect prey (Romanuk and Levings 2003; Romanuk and Levings 2005; Sobocinski et al. 2010).

Diet studies show that juvenile salmon consume fewer insects along armored shorelines (Toft et al. 2007), indicating a reduction in high quality prey. Decreased availability of these prey items may require juvenile salmon to increase their foraging efforts to meet their energy demands, essentially consuming higher quantities of lower-quality prey (Beauchamp et al. 2007; Beauchamp 2009; Duffy et al. 2010). However, increased foraging effort may make these juveniles more conspicuous and susceptible to mortality from predators, as has been demonstrated in lakes (Biro et al. 2003). Predation mortality can influence juvenile salmon survival in some estuarine systems (Willette 2001; Miller et al. 2013), but whether or not shoreline armoring has any relationship to predation in estuarine nearshore habitats is unknown. Shoreline armoring truncates the intertidal gradient resulting in increased water depths when the tide is high, especially where shoreline armoring extends well into the intertidal zone (Toft et al. 2007). Juvenile salmon along armored shorelines may be forced into deeper waters or other less-preferred habitats, where foraging comes at a higher energetic cost if potential prey items are more difficult to locate, and they may encounter increased predation risk (Willette 2001; Biro et al. 2007; Duffy and Beauchamp 2008). Fine-scale investigation of feeding rates of juvenile salmon along armored and unarmored stretches of shoreline in nearshore environments is needed to provide information on the individual behavioral response of juvenile salmon to reduced prey inputs and increased water depths associated with armoring, leading to improved understanding of population-level effects of shoreline armoring.

Fine-scale investigation of juvenile salmon movement and behavior is rare in estuarine nearshore environments (Semmens 2008). Many studies of juvenile salmon in nearshore habitats have used various netting methods to capture fish and obtain information about patterns of abundance, distribution, and feeding habits (Levings et al. 1991; Duffy et al. 2005; Cordell et al. 2011). Direct visual observation of individuals and shoals of juvenile salmon using snorkel surveys has the advantage of recording specific behaviors for large numbers of fish of any body size. Snorkel surveys have been successfully used to study juvenile salmon in estuarine nearshore habitats, employing methods that provided snapshots of fish composition, densities, water column distribution, and behavior but lacked continuous movement and behavior data (Toft et al. 2007; Toft et al. 2013). We developed a method to measure juvenile salmon movement and feeding rates along different natural and altered shoreline types while maintaining temporal continuity in observations, to provide data on habitat use of shallow marine nearshore environments and behavioral responses to shoreline armoring.

As juvenile salmon migrate through nearshore environments, they are likely to experience patches of favorable habitat, e.g. unarmored, shallow segments with high prey production, separated by patches of unfavorable habitat, e.g. deep, armored segments with reduced prey inputs. They may mediate growth by spending proportionally more time feeding when they encounter favorable habitats, rapidly migrating through poor-quality armored habitats. We assessed this potential behavioral response through *in situ* observation of movement rates and feeding behaviors of juvenile salmon along armored and unarmored stretches of shoreline. Specifically, we tested the hypotheses that: (1) juvenile salmon spend proportionally more time feeding along natural and “enhanced” (urban shorelines with restoration of some habitat functions) shorelines compared with armored shorelines; (2) movement rates of juvenile salmon are slower along natural shorelines compared to armored shorelines and are related to behavior (feeding fish will have slower movement rates); and, (3) juvenile salmon along armored shorelines feed at lower rates and swim in straighter paths than juvenile salmon along natural and enhanced shorelines.

Methods

Study sites and species

Study sites were chosen to represent a range of urban and natural shoreline features (Figure 1). Surveys in 2009 were conducted at three sites: (1) Seacrest, an armored beach; (2) Seahurst South, a natural reference beach; and (3) Olympic Sculpture Park (OSP), an enhanced urban beach. Surveys in 2012 were conducted at seven armored-unarmored beach pairs: (1) Site 16: Alki Armored (A) & Unarmored (U); (2) Site 21: Lincoln Park A & U; (3) Site 22: Lowman Beach A & U; (4) Site 13: Marine View Park (MVP) A & U; (5) Site 24: Seahurst North A & U; (6) Site 25:

Seahurst South A & U; and (7) Site 6: Poverty Bay A & U (Fig. 1). We observed four species of juvenile Pacific salmon: chum (*O. keta*), pink (*O. gorbuscha*; 2012 only), Chinook (*O. tschawytscha*) and coho (*O. kistutch*; 2009 only).

2009 snorkel surveys

Weekly snorkel surveys were conducted at each study site at high slack tide so that all potential intertidal salmon habitats were inundated and to minimize the effects of tidal currents on fish movement. Sampling was conducted during months of peak juvenile salmon outmigration, April-August. The minimum horizontal visibility for snorkel surveys was 2.5 m (Toft et al. 2007). Methods were developed in part based on observed juvenile salmon behavioral responses to snorkeler presence during surveys conducted in previous field research from 2002 – 2008 (Toft et al. 2007; 2013), such that we were confident in measuring real fish movement and behavior patterns that were not affected by presence of snorkelers in the water. For each observation, a single snorkeler entered the water and swam along shore until an individual or school of juvenile salmon was seen. If the snorkeler was able to stay with the fish after locating them, she or he gave a signal to an observer on land to mark the start of the observation. The snorkeler initially recorded the following data on the fish: species, count, average size (in 2.5 cm increments), water column position and start time. During each observation, the snorkeler followed the focal fish maintaining distance of approximately 1 m while recording water column position and behavior (Table 1) every minute for the duration of the observation. Ideally, observations lasted 15 min or as long as the fish could be followed.

During the snorkel survey, an observer stood on shore at a reference point of known GPS coordinates. Upon receiving a start signal from the snorkeler, the observer began tracking the snorkeler as a proxy for fish movement using a laser rangefinder that measured distance and compass bearing to the snorkeler. The observer recorded site, date, observation number, start time, reference point and initial position of the snorkeler at the start of each observation, and the position of the snorkeler every 30 seconds for the duration of the observation. All data collected by the observer were spoken into a digital voice recorder.

Movement paths and behaviors were mapped in ArcGIS. Observation points were first plotted in ArcMap and then converted to paths for each observation using the Hawth's tools package. For each observation, the average movement rate (m/s) was calculated as the total path length in meters divided by the duration of observation in seconds. Path complexity was analyzed using a straightness index, D/L, where D is the Euclidean distance between observation start and end points and L is the total length of the path traveled by the organism (Benhamou 2004; Wilson et al. 2007; Almeida et al 2010). Straightness index values range from 0 to 1, with higher values indicating straighter paths.

Juvenile salmon were categorized as chum (CM) or Chinook/coho (CHCO). CHCO were classified in a single taxonomic category because they were sometimes observed together in groups and can be difficult to distinguish, although the majority of these observations are typically Chinook (Toft et al. 2013). No pink salmon were observed in 2009, as juveniles of this species outmigrate through Puget Sound only in even years. Movement rates were analyzed using the nonparametric Kruskal-Wallis test for differences by site, species and school size. Chi-square goodness-of-fit tests were used to analyze the proportion of time juvenile salmon were observed feeding. Straightness indices and movement rates of feeding versus non-feeding schools were compared using Wilcoxon rank-sum tests. Relationships between movement and behavior parameters were examined with Spearman rank correlations.

2012 snorkel surveys

Survey methods employed in 2012 were adapted from 2009 methods to improve the precision of fish position measurements, enable quantification of juvenile salmon feeding rates, and to provide data from paired sites for armored-unarmored comparisons. Snorkel surveys were conducted weekly during the peak of pink/chum outmigration from early April – mid-May, and during the peak of Chinook/coho outmigration from mid-June – early August. Surveys were conducted at high tide to maximize the proximity to the supralittoral zone and/or armoring structures, and the same minimum visibility requirements were used as in 2009.

Surveys began with the snorkeler swimming along 50-m shore-parallel transects at progressive distances from shore (and thus increasing water depths). The snorkeler recorded species, count, body length, water column position, and behavior (Table 1) for all fish observed. Whenever juvenile salmon were encountered, the snorkeler ended the transect and began following the salmon at a distance of approximately one meter.

During the first two minutes of following, the snorkeler allowed the fish to acclimatize to his or her presence while recording onto a dive slate the species, the number of focal fish, and an estimate of fish lengths. After two minutes, the snorkeler marked the starting point of the observation by dropping a small weight with a buoy attached and then followed the focal individual or shoal and counted feeding attempts for fifteen minutes or until the fish could no longer be followed. A waterproof GPS unit attached to the snorkeler's waist belt was used to log the track of the snorkeler as a proxy for the movement path of the fish. At the end of each observation, the snorkeler logged the GPS coordinates of the endpoint and the start point.

Points and tracks were downloaded from the GPS and imported into ArcGIS. Fish tracks were mapped (Fig. 1) and measurements were recorded for the total track distance and the linear distance between start and endpoints using ArcMap. Feeding rates were calculated based on the number of feeding attempts (prey attacks) observed over the duration of the observation.

Juvenile salmon were categorized for analysis as pink-chum (PKCM) because the two species were usually observed together in mixed schools, and Chinook (CH). No juvenile Coho were observed in 2012. Straightness index and movement rate were calculated by the same procedure used for 2009 snorkel surveys. Wilcoxon rank sum tests were used to compare feeding rates, straightness indexes, and movement rates at armored vs. unarmored sites and by taxa group. Spearman rank correlations were used to examine the relationship between movement rate and straightness index.

Results

2009 snorkel surveys

A total of 132 observations were recorded on 31 sampling days between April 28 and August 12, 2009, accounting for 2025 juvenile salmon. Chum salmon were the dominant species observed in April and May, switching to Chinook and coho beginning in June. Chum were smaller on average than CHCO and were observed in significantly larger schools (Wilcoxon rank-sum test for school size, $W = 3304$, $p < 0.00001$) (Table 2). Overall average movement rates and straightness index values showed some variation across study sites (Fig. 2a-b), and were consistently lower for CM than CHCO at all sites (Table 2), but these differences were not statistically significant.

Fish at all habitats had relatively high percentages of feeding behaviors in terms of time observed feeding, calculated as the number of minutes in which behavior was categorized as feeding divided by the total number of minutes of observation (Fig. 2). Feeding behaviors were almost always observed as rapid darts to the surface to attack prey, with fish observed foraging in the middle of the water column in 6 of 132 observations (less than 5%). Chi-square analyses showed that juvenile salmon spent a significantly higher proportion of time feeding than carrying out other behaviors at all study sites ($\chi^2 = 200.5232$, df = 1, $p < 0.00001$). Proportion of time observed feeding was higher for CM than for CHCO (Wilcoxon rank-sum test, $W = 2261.5$, $p = 0.025$) (Table 2). Feeding fish had significantly lower straightness indexes than non-feeding fish; movement rates showed no difference by feeding behavior (Table 3; Fig. 3a-b). Straightness index and movement rate were negatively correlated with proportion of time feeding (Spearman rank correlation, $r_s = -0.16$, $p = 0.036$ and $r_s = -0.32$, $p < 0.0001$, respectively), indicating slower movement rates and more complex movement patterns for feeding fish. School size also differed significantly by behavior category (Wilcoxon rank-sum test, $W = 1565$, $p = 0.00004$), with feeding fish observed in larger schools than non-feeding fish.

2012 snorkel surveys

In 2012, we recorded 26 observations of juvenile salmon on 20 sampling days between April 25 – May 15 and June 10 - August 7, for a total of 874 fish (Table 2). Pink and chum salmon were the dominant species in the earlier sampling period, and Chinook were the dominant species in the later. Average shoal sizes were larger for pink and chum salmon compared to Chinook salmon (Wilcoxon rank-sum test, W = 152.2, p = 0.00002) (Table 2). Juvenile salmon were observed in deeper water at armored sites (average 1.06 m) than at unarmored sites (0.79m) (Wilcoxon rank-sum test, W = 111.5, p = 0.014).

We observed juvenile salmon more frequently at unarmored than at armored sites despite equal sampling effort at both shore types (18 and 8 observations, respectively; chi-squared test, $X^2 = 3.846$, p = 0.049). All of the fish behavior parameters showed some variation among taxa, with PKCM having lower feeding rates, slower movement rates, and higher path straightness (Table 2), but none of these were significant. Movement rate and straightness index were positively correlated (Spearman rank correlation, $r_s = 0.32$, p = 0.049). Average movement rates, average feeding rates, and straightness indices were all higher at armored sites than unarmored sites, but none were significantly different by shore type (Table 3). Both movement rate and straightness index were more variable at unarmored versus armored sites (Fig. 4). As in 2009, fish were almost always observed to attack prey at the surface of the water, with only one observation of an individual feeding in the middle of the water column (less than 5% of observations).

Discussion

We investigated the relationship between movement rates, path complexity, and behavior of juvenile salmon and the influence of shoreline condition, particularly the presence or absence of shoreline armoring, on behavior and movement patterns. Our data show that armoring influences the distribution of juvenile salmon, similar to what has been demonstrated for other fish species in estuarine environments (Toft et al. 2007; Bilkovic and Roggero 2008), as we had fewer observations at armored sites where the juvenile salmon were in deeper water along the shoreline. Although no significant armored-unarmored differences were found in movement rates, feeding behaviors, or path complexity, some trends indicate that shoreline armoring and other physical habitat features potentially influence behavior and movement of juvenile salmon. The range of movement rate and straightness index values suggests that fish at unarmored sites exhibit more diversity of swimming speeds (often including slower speeds) and encompass a broader range of path straightness (particularly at the low end of the spread) than fish at armored sites. Greater shoreline complexity and wider shallow intertidal zones at unarmored sites may enable fish to swim with greater path sinuosity while remaining in shallow water. Unarmored sites with overhanging vegetation produce insects and other invertebrates that provide prey for juvenile salmon; foraging fish at these types of sites may move differently than at armored sites where food sources are more limited (Romanuk and Levings 2003; Toft et al. 2007; Sobocinski et al. 2010).

Our fine-scale patterns of movement and behavior corroborate previous studies indicating that juvenile salmon, particularly chum, pink, and Chinook, use shallow marine nearshore ecosystems for feeding, not just as a migratory corridor (Simenstad 1982; Levings et al. 1991; Duffy et al. 2005; Duffy et al. 2010). In 2009, we found that juvenile salmon spent a significantly higher proportion of time feeding than other behaviors, and in 2012 we found that feeding rates were relatively consistent within species among different sites and shore types. We found that regardless of habitat type, juvenile salmon move at slower rates and in more complex paths when feeding. Rapid growth in early marine residence is important for survival of juvenile salmon (Mortensen et al. 2000; Beamish and Mahnken 2001; Duffy and Beauchamp 2011), thus they may feed at consistently high rates even along suboptimal stretches of shoreline to maximize growth.

The snorkel method developed in this study provides an approach for obtaining continuous information on the behavior and fine-scale movement of small fish in shallow nearshore habitats. Shoreline-oriented juvenile salmon were the target of this study, but the methods presented could be applied to behavior and movement of small fish in other aquatic ecosystems provided water clarity is sufficient. Snorkel surveys represent a non-invasive approach that allows direct observation of fish behavior, but have rarely been used to obtain continuous data on both movement and behavior of fish (Semmens et al. 2005; Nanami and Yamada 2007). Many snorkel survey methods used to assess fish communities in both marine and freshwater ecosystems involve a snorkeler moving past fish along transects or observing fish from a fixed point (Cunjak & Power 1986, Healy & Lonzarich 2000, Riley et al. 2004, Toft et al. 2007), sometimes recording detailed position and instantaneous behavior at a single point in time and space. By following fish, we were able to obtain continuous position and behavior information without handling fish or collecting samples. Snorkel studies that have examined continuous behaviors of juvenile salmon over a given period have focused mainly on competitive interactions of fish in streams (Healy & Lonzarich 2000; Riley et al. 2004) or experimental responses to predation risk (Dionne & Dodson 2002). We showed that snorkel surveys can also be applied to juvenile salmon in estuarine nearshore habitats to study feeding behaviors and movement rates and patterns. Aside from snorkel surveys, most methods for tracking fine-scale fish movement are designed for fish of larger size than the juvenile salmon in our study, involve extensive handling of fish (Semmens 2008; Riding et al. 2009), and are often limited to small numbers of individuals either by the cost in terms of equipment and/or labor, or by the technology (Wilson et al. 2007). The snorkel survey procedure we developed provides an alternative tracking method for small fish in aquatic environments where visibility allows direct observation.

The straightness index of fish paths in our data showed more variation than the movement rate (both by behavior category and shoreline type) and was related to feeding behaviors, as has been found for other organisms (Charoy and Clement 1993; de Knegt et al. 2007; Duffy et al. 2010). Future studies could apply the snorkel methods developed here to determine the relationship between a broader suite of behaviors and movement patterns for juvenile salmon and other fish to enhance the ecological information that can be obtained from observed movement patterns of small fish. Further research focused on following individuals or schools for longer time intervals across multiple shoreline habitats would provide data on behavioral variation across different spatial and temporal scales that could be used to develop models for scaling individual movement paths to population-level rates of swimming and feeding.

In partially urban estuaries like Puget Sound, juvenile salmon encounter a mosaic of shoreline types and habitats, and the quality of habitats occupied in early life may influence survival. Juvenile Chinook salmon survival is positively influenced by rapid growth during early estuarine residence (Duffy and Beauchamp 2011) and the proportion of estuarine habitat in natural condition (Magnusson and Hilborn 2003). Our results show they feed at relatively high rates along armored and unarmored shorelines. Juvenile salmon were more commonly observed at unarmored sites compared to armored sites in 2012, and may spend more time feeding along unarmored shorelines if they preferentially occupy these habitats over armored shorelines. Previous studies have found that different urban shore types influence the distribution of juvenile salmon (Toft et al. 2007), and that enhanced urban shorelines with more shallow nearshore habitat positively influence the feeding frequency of juvenile Chinook salmon relative to adjacent armored shorelines (Toft et al. 2013), but more studies that directly compare juvenile salmon abundances and behaviors in armored and unarmored estuarine nearshore habitats are needed to confirm whether or not any large-scale patterns exist in the response of these fish to armored patches.

Armoring disrupts marine-terrestrial linkages and results in fewer terrestrial inputs to armored shorelines. Terrestrially-derived carbon and prey resources can be important for supporting juvenile salmon in estuaries (Levings et al. 1991; Romanuk and Levings 2005); reduced terrestrial inputs in the form of detritus supporting invertebrate prey, or actual invertebrate prey organisms may represent a detrimental effect of estuarine shoreline armoring for juvenile salmon at the individual level and potentially at the population level. We found some variation in feeding rates between species, but no difference between feeding rates at armored and unarmored shorelines within species. This suggests that the most important distinction between armored and unarmored estuarine habitats for juvenile salmon may be the amount and type of prey available. Future work investigating the scale of variability in prey availability (and support of other habitat functions) between different estuarine shoreline types and different levels of shoreline modification is critical to improving our understanding of the effects of armoring on local feeding conditions for juvenile salmon, which may in turn influence population-level rates of growth and survival (Magnusson and Hilborn 2003; Duffy and Beauchamp 2011). Our observations of juvenile Chinook, coho, chum, and pink salmon feeding primarily at the surface of the water column indicate that future studies of the effects of shoreline armoring on prey availability and habitat quality for these species in shallow nearshore waters should focus on neuston sampling, since this appears to be the preferred prey field.

Table 2. Definition of behavior categories used for juvenile salmon observed in snorkel surveys.

Behavior category	Description
Schooling	Group of fish exhibiting cohesive movement
Feeding	Fish attempting to consume prey items
Swimming	Solitary swimming with no apparent response to snorkeler
Swimming away	Fish swimming at moderate speed away from snorkeler
Fleeing	Fish swimming rapidly away from snorkeler

Table 2. Parameter summary by taxa group for 2009 and 2012 snorkel observations. All values are averages. Taxa groups are abbreviated: CM, chum salmon; CHCO, Chinook and Coho salmon; PKCM, pink and chum salmon; CH, Chinook salmon.

	2009		2012	
Parameter	CM	CHCO	PKCM	CH
Number of observations	41	91	17	9
Total fish count	1501	524	840	34
Group size	37	6	49	4
Individual body length (mm)	62	107	49	69
Track length (m)	84.6	78.4	29.5	85.7
Movement rate (m/s)	0.19	0.22	0.14	0.20
Straightness Index	0.45	0.50	0.72	0.67
Proportion of time feeding (time feeding/total time)	0.78	0.61	n/a	n/a
Feeding rate (# prey capture attempts/fish/min)	n/a	n/a	0.53	1.15

Table 3. Summary of Wilcoxon rank sum tests of behavior parameters for schools categorized as feeding or non-feeding in 2009, and observations at armored or unarmored sites (N = 9 and 17, respectively) in 2012. W is the sum of signed ranks.

Year	Parameter	Group means		W	p-value
2009		Feeding	Non-Feeding		
	Movement Rate	0.22	0.22	853	0.24
	Straightness Index	0.44	0.78	352.5	0.00004*
2012		Armored	Unarmored		
	Straightness Index	0.72	0.67	76	0.61
	Movement rate	0.19	0.15	103	0.14
	Feeding rate	0.84	0.77	93.5	0.36

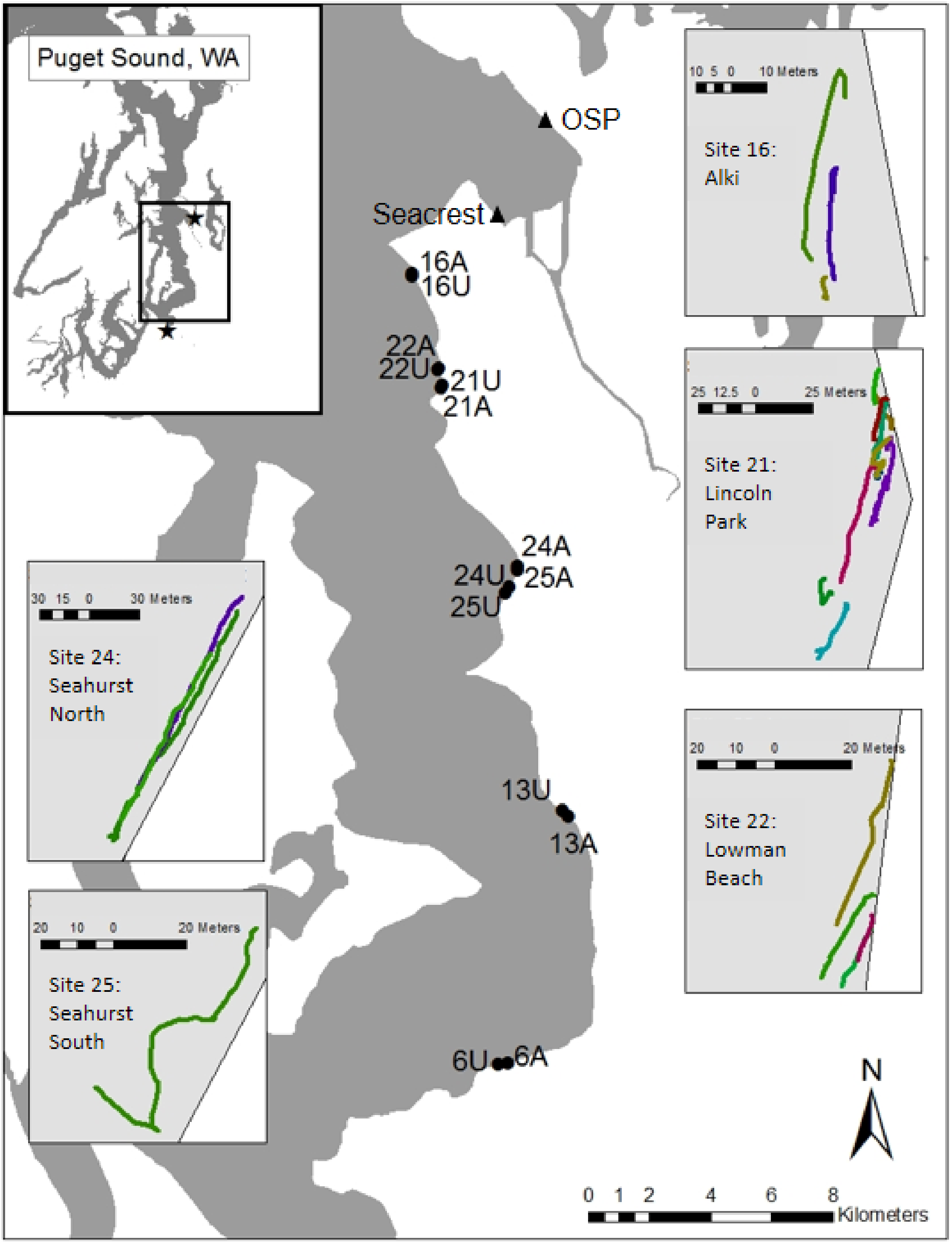

Fig. 5 Map of snorkel sites; sites sampled in 2009 only are indicated with filled triangles, armored (A)-unarmored (U) site pairs from 2012 snorkel surveys are indicated with filled circles. The 25U transect sampled in 2012 is the same as Seahurst sampled in 2009. A subset of fish movement paths obtained by GPS from different snorkel site pairs are shown in insets. Basemap data courtesy of: Washington Dept. of Ecology (WA State Basemap, Place Names), http://www.ecy.wa.gov/services/gis/data/data.htm and Washington State Dept. of Transportation (Shoreline), http://www.wsdot.wa.gov/mapsdata/geodatacatalog/

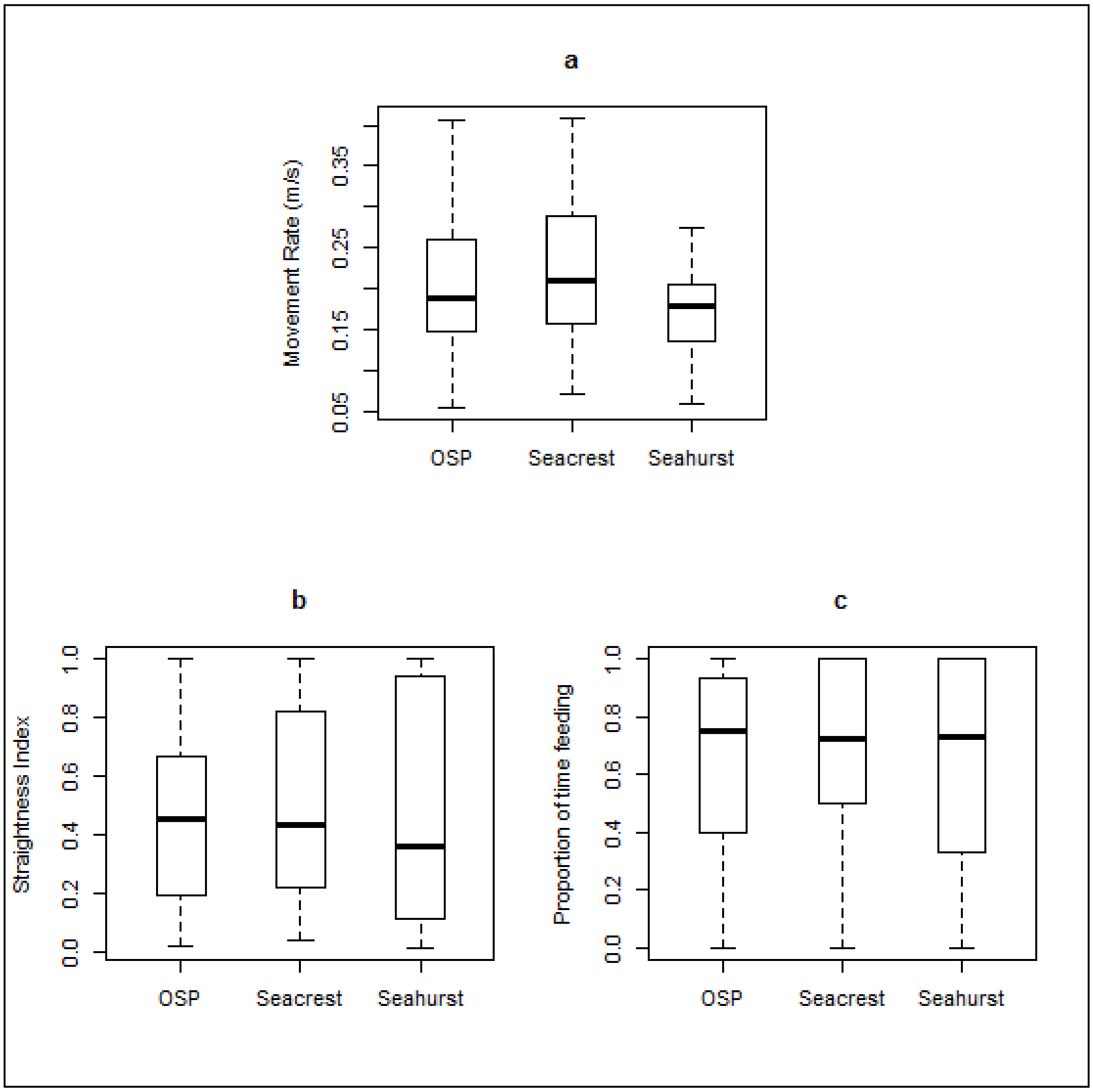

Fig. 2 Summary of 2009 salmon behavior parameters at each site: a) average movement rate; b) average straightness index; c) average proportion of time fish were observed feeding.

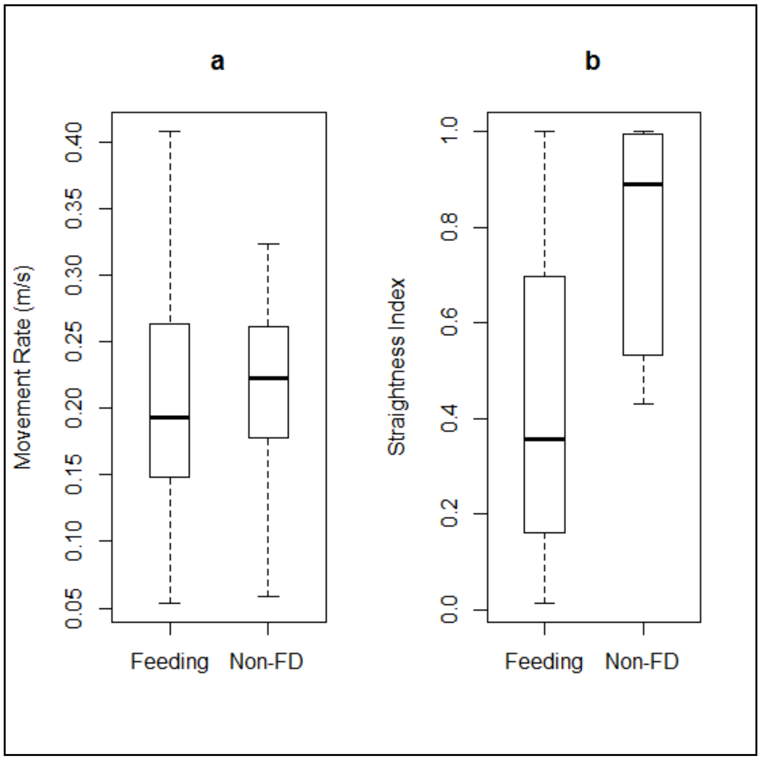

Fig. 3 Summary of 2009 salmon movement parameters by behavior category, feeding or non-feeding: a) average movement rate; b) average straightness index.

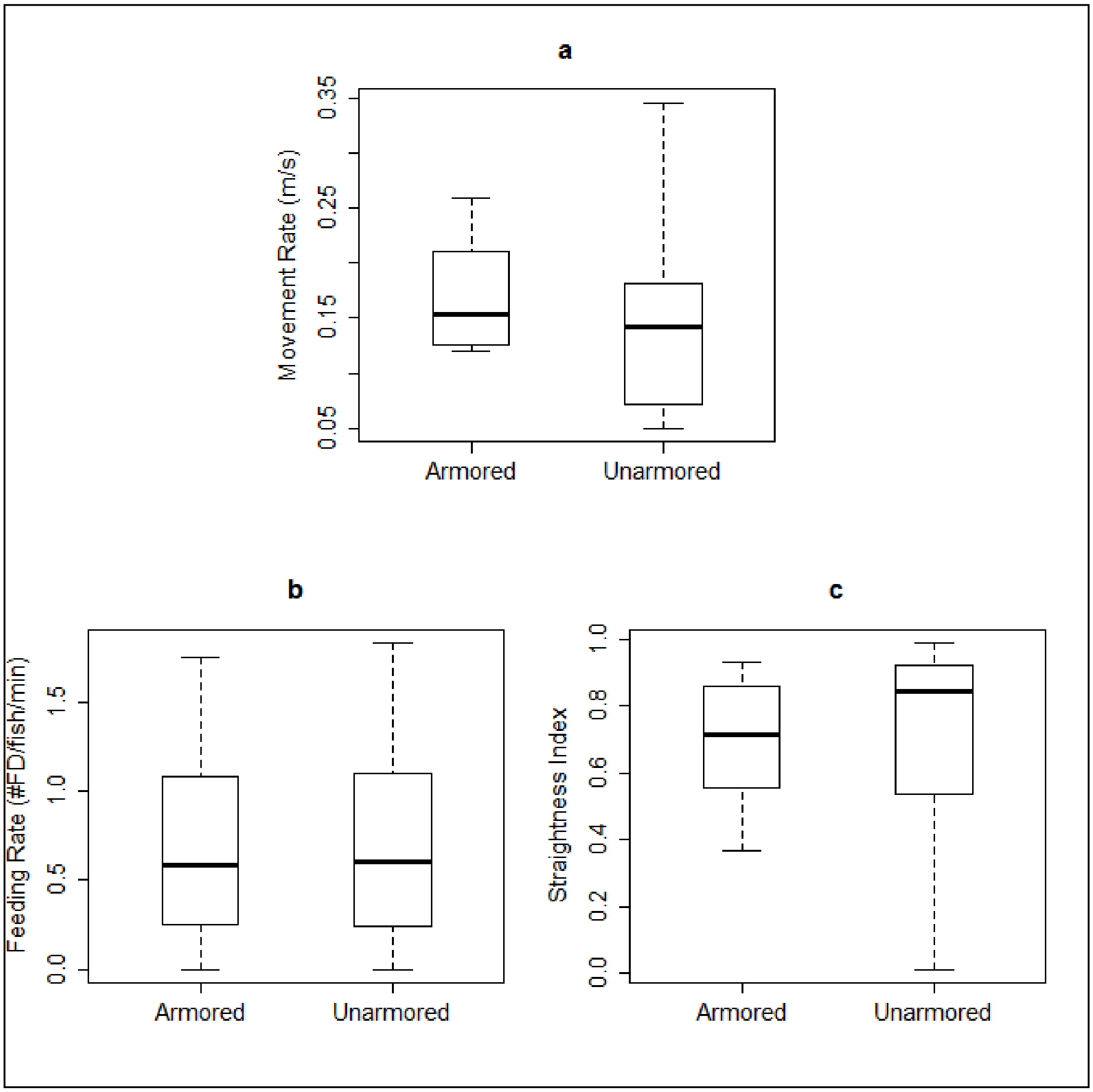

Fig. 4 Boxplots of 2012 snorkel data, comparing armored and unarmored values for behavior parameters: a) movement rate, b) feeding rate, c) straightness index.

Acknowledgements

We thank members of the Wetland Ecosystem Team, especially Claire Levy, Beth Armbrust, Erin Morgan, Lia Stamatiou, and Katie Dowell for assistance with field work. Thanks to Mary Ramirez and Erin Morgan for assistance with processing movement path data in ArcGIS and map creation. Charles Simenstad and Megan Dethier provided valuable reviews of this manuscript prior to submission. We thank Washington Sea Grant, the University of Washington School of Aquatic & Fishery Sciences, the Seattle Art Museum, the City of Seattle, and Seattle Public Utilities for supporting this research.

References

Almeida, P.J.A.L., M.V. Vieira, M. Kajin, G. Forero-Medina and R. Cerqueira. 2010. Indices of movement behavior: conceptual background, effects of scale and location errors. Zoologia 27: 674-680.

Beamish, R.J. and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. Prog Oceanogr 49: 423-437.

Beauchamp, D. A. 2009. Bioenergetic Ontogeny: Linking climate and mass-specific feeding to life-cycle growth and survival of salmon. Pages 53-72 *In* C. Zimmerman and C. C. Krueger, editors. Pacific Salmon: Ecology and Management of Western Alaska's Populations. American Fisheries Society Symposium 70. Bethesda, Maryland.

Beauchamp, D.A., A.D. Cross, J.L. Armstrong, K.W. Myers, J.H. Moss, J.L. Boldt and L.J. Haldorson. 2007. Bioenergetic responses by Pacific salmon to climate and ecosystem variation. N Pac Anadr Fish Comm Bull 4: 257-296.

Benhamou, S. 2004. How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity, or fractal dimension? J Theor Biol 229: 209-220.

Bilkovic, D.M. and M.M. Roggero. 2008. Effects of coastal development on nearshore estuarine nekton communities. Mar Ecol Prog Ser 358: 27-39

Biro, P.A., M.V. Abrahams, and J.R. Post. 2007. Direct manipulation of behaviour reveals a mechanism for variation in growth and mortality among prey populations. Anim Behav 73: 891-896

Biro, P.A, J.R. Post, and E.A. Parkinson. 2003. From individuals to populations: Prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84: 2419-2431.

Charoy, C. and P. Clement. 1993. Foraging behavior of *Brachionus calyciflorus* (Pallas) - variations in the swimming path according to presence or absence of algal food (*Chlorella*). Hydrobiologia 255: 95–100.

Cordell, J.R., J.D. Toft, A. Gray, G.T. Ruggerone, and M. Cooksey. 2011. Functions of restored wetlands for juvenile salmon in an industrialized estuary. Ecol Eng 37: 343-353.

Cunjak, R.A. and G. Power. 1986. Winter habitat utilization by stream resident brook trout (*Salvelinus frontinalis*) and brown trout (*Salmo trutta*). Can J Fish Aquat Sci 43: 1970-1981.

De Knegt, H.J., G.M. Hengeveld, F. van Langevelde, W.F. de Boer and K.P. Kirkman. 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. Behav Ecol 18: 1065-1072.

Dionne, M. and J.J. Dodson. 2002. Impact of exposure to a simulated predator (*Mergus merganser*) on the activity of juvenile Atlantic salmon (*Salmo salar*) in a natural environment. Can J Zoolog 80: 2006- 2013.

Duffy, E.J. and D.A. Beauchamp. 2008. Spatial patterns of predation on juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. T Am Fish Soc 137: 165-181.

Duffy, E.J. and D.A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, WA. Can J Fish Aquat Sci 68: 232-240.

Duffy, E.J., D.A. Beauchamp, and R.M. Buckley. 2005. Early marine life history of juvenile Pacific salmon in two regions of Puget Sound. Estuar Coast Shelf S 64: 94-107.

Duffy, E.J., D.A. Beauchamp, R.M. Sweeting, R.M., R.J. Beamish, and J.S. Brennan. 2010. Ontogenetic diet shifts of juvenile Chinook salmon in nearshore and offshore habitats of Puget Sound. T Am Fish Soc 139: 803-823.

Duffy, K.J., X.H. Dai, G. Shannon, R. Slotow, and B. Page. 2011. Movement patterns of African elephants (*Loxodonta africana*) in different habitat types. S Afr J Wildl Res 41: 21-28.

Healey, M.C. 1982. Juvenile Pacific salmon in estuaries: the life support system. In: Estuarine Comparisons (V.S. Kennedy, ed.). Academic Press, New York, pp 315-341.

Healy, B.D. and D.G. Lonzarich. 2000. Microhabitat use and behavior of overwintering juvenile coho salmon in a Lake Superior tributary. T Am Fish Soc 129: 866-872.

Johnson, L.L., G.M. Ylitalo, C.A. Sloan, B.F. Anulacion, A.N. Kagley, M.R. Arkoosh, T.A. Lundrigan, K. Larson, M. Siipola, and T.K. Collier. 2007. Persistent organic pollutants in outmigrant juvenile Chinook salmon from the Lower Columbia Estuary, USA. Sci Total Environ 374: 342-366.

Johnson, L.L., G.M. Ylitalo, M.R. Arkoosh, A.N. Kagley, C. Stafford, J.L. Bolton, J. Buzitis, B.F. Anulacion, and T.K. Collier. 2007. Contaminant exposure in outmigrant juvenile salmon from Pacific Northwest estuaries of the United States. Environ Monit Assess 124: 167-194.

Koehler, M.E., K.L. Fresh, D.A. Beauchamp, J.R. Cordell, C.A. Simenstad. 2006. Diet and bioenergetics of lake-rearing juvenile Chinook salmon in Lake Washington. Transactions of the American Fisheries Society 135:1580-1591.

Levings, C.D., K. Conlin, and B. Raymond. 1991. Intertidal habitats used by juvenile Chinook salmon (*Oncorhynchus tshawytscha*) rearing in the north arm of the Fraser River estuary. Mar Pollut Bull 22: 20-26.

Loge, F.J., M.R. Arkoosh, T.R. Ginn, L.L. Johnson, and T.K. Collier. 2005. Impact of environmental stressors on the dynamics of disease transmission. Environ Sci Technol 39: 7329-7336.

Magnusson, A. and R. Hilborn. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the US Pacific Coast. Estuaries 26: 1094-1103.

McClure, M.M., S.M. Carlson, T.J. Beechie, G.R. Pess, J.C. Jorgensen, S.M. Sogard, S.E. Sultan, D.M. Holzer, J. Travis, B.L. Sanderson, M.E. Power, and R.W. Carmichael. 2008. Evolutionary consequences of habitat loss for Pacific anadromous salmonids. Evol Appl 1: 300-318.

Miller, J.A., D.J. Teel, A. Baptista, and C.A. Morgan. 2013. Disentangling bottom-up and top-down effects on survival during early ocean residence in a population of Chinook salmon (*Oncorhynchus tshawytscha*). Can J Fish Aquat Sci 70: 617-629.

Mortensen, D., A. Wertheimer, S. Taylor and G. Landingham. 2000. The relation between early marine growth of pink salmon, *Oncorhynchus gorbuscha*, and marine water temperature, secondary production, and survival to adulthood. Fish B-NOAA 98: 319-335.

Nanami, A. and H. Yamada. 2007. Size and spatial arrangement of home range of checkered red snapper *Lutjanus decussatus* (Lutjanidae) in an Okinawan coral reef determined using a portable GPS receiver. Mar Biol 153: 1103-1111.

Riding, T.A.C., T.E. Dennis, C.L. Stewart, M.M. Walker, and J.C. Montgomery. 2009. Tracking fish using 'buoy-based' GPS telemetry. Mar Ecol Prog Ser 377: 255-262.

Riley, S.C., H.J. Fuss, and L.L. LeClair. 2004. Ecological effects of hatchery-reared juvenile Chinook and coho salmon on wild juvenile salmonids in two Washington streams. N Am J Fish Manage 24: 506-517.

Romanuk T.N. and C.D. Levings. 2003. Associations between arthropods and supra-littoral ecotone: dependence of aquatic and terrestrial taxa on riparian vegetation. Environ Entomol 32: 1343–1353.

Romanuk, T.N. and C.D. Levings. 2005. Stable isotope analysis of trophic position and terrestrial vs. marine carbon sources for juvenile Pacific salmonids in nearshore marine habitats. Fisheries Manag and Ecol 12: 113-121.

Romanuk, T.N. and C.D. Levings. 2006. Relationships between fish and supralittoral vegetation in nearshore marine habitats. Aquat Conserv 16: 115-132.

Shaffer, J.A., M. Beirne, T. Ritchie, R. Paradis, D. Barry, and P. Crain. 2009. Fish habitat use response to anthropogenic induced changes of physical processes in the Elwha estuary, Washington, USA. Hydrobiologia 636: 179-190.

Semmens, B.X. 2008. Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. Can J Fish Aquat Sci 65: 2053-2062.

Semmens, B.X., D.R. Brumbaugh, and J.A. Drew. 2005. Interpreting space use and behavior of blue tang, *Acanthurus coeruleus*, in the context of habitat, density, and intra-specific interactions. Environ Biol Fish 74: 99-107.

Sergeant, C.J. and D.A. Beauchamp. 2006. Effects of physical habitat and ontogeny on lentic habitat preferences of juvenile Chinook salmon. T Am Fish Soc 135: 1191-1204.

Simenstad, C.A., K.L. Fresh and E.O. Salo. 1982. The role of Puget Sound estuaries in the life history of Pacific salmon: an unappreciated function. In: Estuarine Comparisons (V.S. Kennedy, ed.). Academic Press, N.Y. pp. 343-364.

Simmons, R.K., T.P. Quinn, L.W. Seeb, D.E. Schindler, and R. Hilborn. 2013. Role of estuarine rearing for sockeye salmon in Alaska (USA). Mar Ecol Prog Ser 481: 211-223.

Sobocinski, K.L., J.R. Cordell, and C.A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuar Coast 33: 699-711.

Stein, J.E., T. Hom, T.K. Collier, D.W. Brown, and U. Varanasi. 1995. Contaminant exposure and biochemical effects in outmigrant juvenile Chinook salmon from urban and nonurban estuaries of Puget Sound, Washington. Environ Toxicol Chem 14: 1019-1029.

Tabor, R.A., K.L. Fresh, R.M. Piaskowski, H.A. Gearns, and D.B. Hayes. 2011. Habitat use by juvenile Chinook salmon in the nearshore areas of Lake Washington: effects of depth, lakeshore development, substrate, and vegetation. N Am J Fish Manage 31: 700-713.

Thorpe, J.E. 1994. Salmonid fishes and the estuarine environment. Estuaries 17: 76-93.

Toft, J.D., J.R. Cordell, C.A. Simenstad, and L.A. Stamatiou. 2007. Fish distribution, abundance, and behavior along city shoreline types in Puget Sound. N Am J Fish Manage 27:465-480.

Toft, J.D., A.S. Ogston, S.M. Heerhartz, J.R. Cordell, and E.E. Flemer. 2013. Ecological response and physical stability of habitat enhancements along an urban armored shoreline. Ecol Eng 57: 97-108.

Willette, T.H. 2001. Foraging behaviour of juvenile pink salmon (*Oncorhynchus gorbuscha*) and size-dependent predation risk. Fish Oceanogr 10: 110-131

Wilson, R. P., N. Liebsch, I.M. Davies, F. Quintana, H. Weimerskirch, S. Storch, K. Lucke, U. Siebert, S. Zankl, G. Müller, I. Zimmer, A. Scolaro, C. Campagna, J. Plötz, H. Bornemann, J. Teilmann, and C.R. McMahon. 2007. All at sea with animal tracks; methodological and analytical solutions for the resolution of movement. Deep-Sea Res Pt II 54:193–210.

Wissmar, R.C. and C.A. Simenstad. 1988. Energetic constraints of juvenile chum salmon (*Onchorhynchus keta*) migrating in estuaries. Can J Fish Aquat Sci 45: 1555-1560.

WSDOE (Washington State Department of Ecology). Puget Sound Home Page. http://www.ecy.wa.gov/puget_sound/index.html

Chapter 5. Differences in abundance and behavior of terrestrial birds on armored and unarmored beaches

Authors

Sarah M. Heerhartz, Megan N. Dethier, and Jason D. Toft

Abstract

Beach wrack subsidies support high densities of primary consumers, such as talitrid amphipods and insects. In many ecosystems, these organisms in turn provide food for mobile secondary consumers, including shorebirds, reptiles, and small mammals. The aim of this study was to document the use of beach wrack and log zones as foraging habitat for terrestrial birds that occupy marine riparian vegetation and travel to the beach to make use of abundant invertebrate prey resources. We conducted bird observations focused along upper intertidal transects at six armored-unarmored beach pairs in summer during two study years. Song Sparrows (*Melospiza melodia*) were the most common bird observed on unarmored beaches, while American Crows (*Corvus brachyrhyncos*) were the most common species observed on armored beaches. Birds observed on unarmored beaches foraged among beach wrack and logs and consumed talitrid amphipods and insects found there. Previous research has shown wrack zones to be important foraging habitats for shorebirds on sandy beaches; this study documents use of these habitats including driftwood by terrestrial birds, indicating that these secondary consumers benefit from beach wrack subsidies.

Introduction

Ecotones occur where different ecosystems converge and may represent discrete boundaries for some ecosystem components (e.g. nutrients, detritus, organisms) and gradients for other components. Many cases of organic subsidies that originate in one ecosystem, are transported (or actively move) across ecotones, and increase primary productivity or consumer densities in recipient ecosystems have been demonstrated, for example aquatic-emergent insects from streams that are fed upon by forest birds (Nakano and Murakami 2001), and invertebrates associated with marine detritus on sandy coasts that are consumed by lizards (Barrett et al. 2005; Wright et al. 2013), shorebirds (Dugan et al. 2003), and rodents (Stapp and Polis 2003).

We will use the term nearshore ecotone to refer to the interface between marine and terrestrial ecosystems characterized by low-wave-energy, mixed-sediment beaches fringed with riparian vegetation and centered on the intertidal zone. These types of ecotones are relatively understudied, but represent potential for subsidization for primary consumers in the form of detritus from both marine and terrestrial sources deposited on the upper beach as the tide ebbs (i.e. beach wrack and logs); and in the form of prey for secondary consumers. For example, juvenile salmon (Onchorhynchus spp.) in shallow nearshore waters are know to consume riparian insects, and terrestrial material has been shown to be a major carbon source for these fish (Romanuk and Levings 2010), and many species of birds consume fish and other marine resources (Dierschke and Bairlein, 2004; Craik et al. 2011).

Birds are highly mobile organisms that can move between some ecosystems, potentially acting as vectors of nutrients or other materials across ecotones (Polis and Hurd 1996) or benefitting from resources produced in multiple ecosystems (Nakano and Murakami 2001; Nagelkerken et al. 2008). The abundance, species composition, and behavior of birds within a particular ecotone may be influenced by specific features of the interface or boundary. Previous research has shown that some birds avoid edges associated with anthropogenic land use; for example Laiolo and Rolando (2005) found that birds associated with forest-pasture ecotones in the Alps avoided forest-ski run ecotones, likely because of the greater complexity of vegetation and edge shape and width in the former, compared to more high-contrast, linear edge in the latter. Other birds, such as crows, are associated with impervious surfaces and maintained vegetation characteristic of anthropogenic land use (Withey and Marzluff 2009); these species may respond differently to modified edges.

Riparian zones are interfaces between terrestrial and aquatic systems that provide multiple habitat functions for a diverse array of birds along streams and other ecotones including marine shorelines. Functions of these transitional habitats could include refugia from predators, spaces for perching and roosting, habitat for nesting, and production of edible plants and insect prey (Nakano and Murakami 2001; Brennan and Culverwell 2004; Uesugi and Murakami 2007; Christie et al. 2008). Observations of bird behavior in marine riparian zones are rare, and there are very few quantitative data related to habitat functions such as fitness or survival benefits accruing to birds there. Aquatic subsidies to birds utilizing stream habitats (Christie et al. 2008; Uesugi and Murakami 2007), sandy beaches (Dugan et al. 2003; Hubbard and Dugan 2003), and inland seas (Brehme et al. 2009) for foraging have been demonstrated; similar types of subsidies as well as other habitat functions may be important along marine shorelines as well, but few studies have investigated this.

Much of the natural (undisturbed) nearshore ecotone of Puget Sound, WA, USA is characterized by riparian vegetation and accumulation along the upper shore of abundant logs and beach wrack (composed of a mix of debris from marine macrophytes, algae, and terrestrial plants; Heerhartz et al., in press [Chapter 2]). The beach below this wrack zone tends to have relatively bare sediment (typically a mix of sand, pebbles, and cobbles) composing the active beach face, and algal and seagrass beds in the low intertidal to subtidal zone. Upper intertidal wrack zones can be important foraging habitats for shorebirds (Dugan et al. 2003) that feed on talitrid amphipods, insects and other invertebrates. The role of beach wrack as a subsidy to wave-exposed sandy beaches has been well-established. Recent research has shown that wrack also plays an important role in fetch-limited estuarine nearshore ecosystems (Sobocinski et al. 2010; Heerhartz et al, in press [Chapter 2]; Heerhartz et al, in prep [Chapter 3]). On these estuarine shorelines, not just shorebirds but also terrestrial birds may occupy riparian habitats and utilize beach wrack for foraging on abundant prey resources such as talitrid amphipods and insects.

Shoreline armoring is an anthropogenic feature of many coastal ecosystems, including about 27% of the total shoreline length of Puget Sound. Armoring is arguably used to prevent coastal erosion and protect human property and infrastructure along shorelines. One ecological consequence of armoring is that it disrupts connectivity across the ecotone between marine and terrestrial ecosystems. Shoreline armoring results in loss of riparian vegetation, reduced abundances of logs and wrack in the upper intertidal (Heerhartz, et al., in press[Chapter 2]), and fewer riparian and wrack-associated invertebrates (Sobocinski et al. 2010; Heerhartz, et al., in prep, [Chapter 3]) available as prey for birds and other consumers. Whether or not these differences affect birds that typically occupy marine riparian habitats is unknown. We hypothesized that the intact marine-terrestrial linkage at unarmored sites supports foraging in the nearshore ecotone by both shorebirds and terrestrial passerine birds (hereafter, songbirds), while adjacent armored sites do not provide this function.

We used focal animal sampling (Altmann 1974) to record behaviors of individual birds occupying the marine-terrestrial ecotone at paired armored and unarmored beaches. Of particular interest was the proportion of time spent foraging compared to other behaviors. Our objective was to record bird species observed, their exact location (substrate), and behavior within the ecotone and to identify differences in bird use between armored and unarmored beaches, specifically: (1) species and numbers of birds observed; and (2) the proportion of time focal individuals spend feeding versus other behaviors (resting, in transit).

Methods

Study sites

Bird surveys were conducted at six armored-unarmored beach pairs, or twelve total transects (Table 1; see Fig. 1, Chapter 2 for map): Seahurst North (24A/U); Seahurst South (25 A/U); Marine View Park (13 A/U); Poverty Bay (6 A/U); Lincoln Park (21 A/U); and Lowman Beach (22A/U). Armored beaches either had sloped riprap or vertical concrete along the upper beach encompassing a range of tidal elevations (Table 1). Most of the beaches surveyed were in public parks (24A/U, 25A, 13U, 21A/U, 22 A/U), but a few were on private property that we gained permission to access (25U, 13A, 6A/U). One beach that was categorized as unarmored (21U) for pairing actually had sloped riprap that was mostly overgrown with dunegrass or covered by driftwood logs in the supratidal, while its companion armored beach had vertical concrete at a slightly lower elevation. This pair also had a public walking path between the supralittoral/armoring and backshore riparian vegetation, but some of the larger trees still shaded both beaches. Pairs 21 and 22 are within the city limits of Seattle, WA, and are within a mostly-armored drift cell. The other pairs are located south of Seattle in areas with less shoreline armoring. Beaches 6U, 13U, 24U, and 25U had overhanging vegetation along 90 – 100% of the upper intertidal. Beach aspects were consistent within pairs and included northwest (pair 6), west (pairs 21, 22, 24, and 25), and southwest (pair 13). There was some variability in the amount of wrack between all beaches, but the major pattern of difference was between armored and unarmored beaches, with significantly more wrack, a greater proportion of terrestrial plant material in wrack, and more logs at unarmored beaches (Heerhartz et al., in press; Chapter 2).

Survey methods

We conducted bird surveys to record the species occurrence, abundance, and the amount of time devoted to specific behaviors. Surveys were conducted at each beach along a 50 m transect centered on the most recent wrack line but encompassing the intertidal zone from water line to riparian vegetation. Transects were divided into segments if the entire transect was not visible from a single vantage point (e.g., due to trees fallen onto the beach), in which case vantage points were selected ahead of time and equal amounts of time were spent surveying from each. The minimum survey duration was seven minutes per segment. On average, we spent 20 minutes at each transect. We recorded wind/sea state (Beaufort scale), precipitation, cloud cover, air temperature, and tide height and stage (high, low, rising, falling) prior to the start of observations at each transect. If it was raining or windy (> 15 knots, moderate sized tree branches and small trees moving), or other environmental factors appeared to be affecting bird activity (for example high volumes of human traffic), we did not conduct surveys on that day.

We surveyed birds weekly at each beach pair from mid-April to mid-May and mid-June to early August in 2012, and twice per week during the last two weeks of June and August in 2013. Surveys in 2012 were conducted when the tidal elevation was above +2 m MLLW at variable times of day, concurrent with snorkel observations (Chapter 4), while in 2013 we began all surveys within 30 minutes after sunrise. We controlled for time of day and related environmental conditions between armored and unarmored transects within a pair by surveying birds either simultaneously with two observers, one at each transect, or with the second transect immediately following the first.

We used focal-animal surveying to gather quantitative data on how birds use their time in the wrack zone of beaches. Individual or small groups of focal birds were observed in detail until they left the observation area; because birds were observed until they left the observation area (i.e., flew away to an area outside of the transect), it is unlikely that focal individuals were counted more than once during a survey. In 2013, we added counts of the number of feeding attempts (pecks) for foraging individuals to estimate feeding rates as number of pecks per minute (Dierschke 1993). For analysis, behaviors were categorized as foraging, traveling (included hopping, flitting, and walking), and perching. Other behaviors that were only rarely observed, such as gathering nest materials and aggression toward conspecifics, were noted but excluded from data analysis. In the following text, we will refer to focal bird observations as observations, and the sum of time spent on a given transect on a single sampling date either observing birds or scanning for birds as surveys.

Data Analysis

Bird species were categorized into broader taxonomic groups for analysis (Table 1). The proportion of total survey time during which birds were observed was calculated as the minutes of focal bird observation/minutes of survey. We also standardized the number of individuals observed by survey minute (count of individuals/minutes of survey). We used paired t-tests to analyze differences in the average proportion of survey time in which birds were observed and the number of individuals observed per minute between years (with beaches as replicates) and between armored and unarmored beaches (with sites as replicates). We tested for differences in proportion of time birds were observed in different behavior categories using Chi-square tests.

Results

Overall we observed 10 species of songbirds and 6 other species of birds at the study sites (Table 1). Crows (*Corvus brachyrhyncos*) and Song Sparrows (*Melospiza melodia*) were the most common species observed. Because the majority of our observations were conducted outside of peak migration times, most of the birds we observed were year-round or summer resident species. We observed three non-indigenous species that are well-established in the Puget Sound region: Rock Pigeon (*Columba livia*), Common Starling (*Sturnus vulgaris*), and House Sparrow (*Passer domesticus*); all others observed are indigenous. The majority of birds we observed (11 of the 16 species) are ground-foraging consumers of seeds and/or insects and other invertebrates. We also observed two aerial foragers: the Barn Swallow (*Hirundo rustica*), which eats insects and an unspecified Hummingbird (Trochilidae), which consumes nectar, and two foliage gleaners: the Chestnut-backed Chickadee (*Poecile rufescens*), which eats insects, and the American Goldfinch (*Spinus tristis*), which eats seeds.

Although our surveys were conducted at different times of day in 2012 and 2013, there were no differences in average proportion of survey time that birds were observed (paired t-test between years, beaches as replicates, p = 0.81) or the average number of focal bird observations made per unit time (paired t-test between years, beaches as replicates, p = 0.21). Thus, data from all time periods are pooled for analyses. Our method of dividing transects when the entire transect could not be seen from a single vantage point led to approximately 25% more time spent at unarmored beaches (1035 unarmored vs. 825 armored total minutes) due to the increased habitat complexity therein, which often required several vantage points to see around overhanging trees. Similarly, the sum of minutes of focal animal observation was 25% more at unarmored beaches (armored, 190 minutes; unarmored, 239 minutes), however the total proportion of survey minutes in which birds were observed was equal for both beach types (total observation minutes/total survey minutes = 0.23 for both).

The average proportion of survey minutes during which songbirds (crows, sparrows, and other passerines) were observed on the transect was significantly greater at unarmored beaches than armored beaches (paired t-test, sites as replicates, unarmored mean 0.20, armored mean 0.13, $p = 0.03$; Fig. 1). We observed significantly more songbirds (i.e., more focal animal observations) on average per survey minute at unarmored beaches (mean 0.10 birds per survey minute; Fig 2) than armored beaches (armored mean 0.05 birds per survey minute; one-tailed, paired t-test, $p = 0.0003$). Seagulls were only observed at armored beaches, while other terrestrial birds and shorebirds (Table 1) were only observed at unarmored beaches (Fig 2).

The proportion of observed time of focal bird behaviors differed between armored and unarmored beaches (Fig. 3). Overall, birds spent proportionally more time perching (63% of total time) than foraging (29% of total time) at armored beaches compared to unarmored beaches, where birds spent 37% of the total time observed perching and 45% of total time observed foraging. Proportion of observed time spent traveling was similar at both armored (17%) and unarmored (20%) beaches. A Chi square test on actual minutes observed in each behavior (with expected values corrected for the longer observations at unarmored beaches) showed that this focus on foraging time at unarmored beaches was significant (Chi Square = 12.86, 2 d.f., $p < 0.01$).

When songbirds were analyzed separately (Fig. 4), this difference was even more clear; songbirds spent proportionally more time foraging at unarmored beaches (54% of total time) than armored beaches (37% of total time). Songbirds at armored beaches spent proportionally more time perching either on the beach or on the armoring structure (29% of observed time) than on unarmored beaches (15% of total time), where perching most often occurred on logs or riparian vegetation overhanging the wrack zone. These behavioral differences associated with armoring were again significant (Chi Square = 6.04, 2 d.f., $p < 0.05$).

Feeding rates (rate of attempts: number of pecks/duration of observation in minutes) were calculated for a total of 35 individuals (10 crows, 17 sparrows, 8 other passerines; Table 1), with an overall average of 11.2 pecks per minute and high variability about the mean (standard deviation (SD) 10.4). There were no differences in average feeding rates between armored (mean 11.6 pecks per minute, SD 10.8, N = 9) and unarmored (mean 11.5 pecks per minute, SD 10.6, N = 26) beaches, but there were fewer total foraging observations at armored beaches (Fig. 4).

Discussion

Our results show that the species composition and behaviors of birds occurring along armored estuarine shorelines differ from those along unarmored shorelines, with a greater proportion of sparrows and other small insectivores and seed-eaters at unarmored beaches, and proportionally more crows, gulls, and other ground-foraging generalists at armored beaches. There are several potential mechanisms driving this pattern. Firstly, lower abundances of wrack and logs at armored beaches (Chapter 2; Heerhartz et al., in press) mean fewer wrack-associated invertebrates, particularly talitrid amphipods, flies, and beetles (Chapter 3) as well as less terrestrial plant material to be eaten by birds. Secondly, armoring disrupts or removes marine riparian vegetation (Chapter 2; Heerhartz et al., in press), thereby reducing shore access for songbirds and other terrestrial birds. Finally, logs were often used by sparrows, finches, and other small ground-foraging birds for perching or foraging at unarmored beaches; absence or greatly reduced numbers of logs may affect which species use intertidal habitats at armored beaches.

Many of the robins, song sparrows, and other songbirds we observed accessed the beach directly from riparian vegetation. When natural riparian vegetation is not present, there are fewer birds in the vicinity and no nearby points of entry and exit. Riparian vegetation probably provides an easy refuge from predators for small songbirds; the abundance of logs on unarmored beaches may also provide shelter. Riprap boulders used for armoring at some sites could potentially provide shelter, although we did not observe many sparrows or other small terrestrial/passerine birds among riprap. In contrast, seagulls tended to access our study beaches from the water, and were more likely to use upper beach habitats for perching rather than foraging. Crows were observed to forage in beach wrack, but they also often accessed the wrack line after foraging lower on the beach, and thus were less likely to be affected by the removal of riparian vegetation.

Few studies have documented birds foraging in beach wrack and among logs in the upper intertidal zone of estuarine beaches. On wave-exposed sandy beaches, shorebird abundance correlates with abundance of wrack and wrack-associated invertebrates (Dugan et al. 2003). We suggest that a similar relationship exists for songbirds along estuarine shorelines bordered by riparian zones, with beach wrack providing an important foraging resource. Birds used armored shorelines mainly for perching, while they used unarmored beaches mainly for foraging. Similar to juvenile salmon (Chapter 4), we observed birds to forage at similar rates at both armored and unarmored beaches but to spend a significantly greater proportion of time foraging on unarmored beaches. Further research on this topic is needed to develop a clearer picture of the cumulative effects of shoreline armoring on estuarine nearshore ecosystems, particularly how shoreline armoring influences birds that may utilize beach wrack subsidies.

Future studies should investigate the significance of loss of foraging access and resources for sparrows and other small passerine/terrestrial birds along armored shorelines. Because birds are highly mobile, they likely minimize potential effects of armoring through individual behavior (e.g. avoid armored beaches, move to preferred habitats). However in developed areas, birds may have to travel farther to find patches of suitable habitat, which would come with an energetic cost. Migratory birds may use nearshore habitats differently than resident birds, or at different times of year. We noticed a few cup nests in riparian vegetation directly overhanging the beach; birds nesting in these habitats may rely more heavily on beach wrack as a food source due to its proximity to nests. A related topic for investigation is whether birds nesting in riparian zones utilize any wrack material in constructing their nests.

Whether or not beach wrack and associated invertebrates represent an organic subsidy to terrestrial birds is an ecologically significant question. Our observations of terrestrial birds foraging among beach wrack and logs and consuming talitrid amphipods and insects indicates that the potential for subsidization exists. Our results suggest that beach wrack and associated prey items increase consumer densities in the nearshore ecotone at unarmored beaches relative to armored beaches. The next step is to determine whether any species are more abundant within the ecotone relative to adjacent upland habitats.

Restoration of riparian zones along estuarine shorelines may benefit birds that use these habitats. Along armored shorelines that can't be restored to natural conditions, planting vegetation and anchoring logs could be used to enhance habitat functions of foraging and perching for a variety of terrestrial birds. Further knowledge of the importance of riparian zones, logs, and beach wrack as habitat for different bird species in nearshore ecotones is needed for understanding broad-scale effects of shoreline armoring and developing appropriate restoration or conservation strategies that account for connectivity between aquatic and terrestrial ecosystems.

Tables and Figures

Table 1 Summary of physical characteristics and vegetation parameters of survey beaches. Beach type refers to armored, A, or unarmored, U. Beach width is the measured distance in meters from the armoring or bluff toe to Mean Low Water. Maximum elevation is the height in meters above Mean Lower Low Water. Armor type categories: vertical concrete, VC; sloping riprap, SR; none, N. Bank type was categorized as either vegetated bluff, VB, or developed, D. Supratidal vegetation categories: blackberry, BL; dunegrass, D; none, N. Backshore vegetation refers to vegetation immediately landward of the supratidal zone or armoring structure; categories: shrubs, S; trees, T; lawn, L.

Pair	Beach Type	Beach width (m)	Maximum elevation (m)	Beach slope	Armor type	Bank type	Vegetation	
							Supra-tidal	Back-shore
6	A	23.5	3.77	0.053	VC	D	N	L
	U	25.7	3.70	0.043	N	VB	N	T
13	A	20.0	2.86	0.100	VC	D	N	L
	U	27.2	4.00	0.115	N	VB	BL	T
21	A	23.5	3.69	0.088	VC	VB	N	T
	U	25.0	3.84	0.103	SR	VB	D	T
22	A	50.0	2.64	0.036	VC	D	N	L
	U	50.3	4.85	0.043	N	D	D	L
24	A	18.5	2.28	0.041	SR	D	N	L
	U	23.3	4.14	0.128	N	VB	D	T
25	A	27.9	2.69	0.039	SR	D	N	L
	U	28.0	4.16	0.114	N	VB	BL	T

Table 2 Summary of all bird taxa observed; the number of observations for each taxa are listed in columns U, unarmored, and A, armored, with a dash indicating no observations. Species for which feeding rates were calculated for focal individuals are indicated with a *.

Taxa group	Common name	Scientific name	U	A
Corvidae	American Crow	*Corvus brachyrhynchos**	23	31
Emberizidae	Song Sparrow	*Melospiza melodia**	40	5
	American sparrow, unspecified	Emberizidae	12	6
	White-Crowned Sparrow	*Zonotrichia leucophrys**	1	-
Other Passerine	American Goldfinch	*Spinus tristis**	1	2
	American Robin	*Turdus migratorius**	6	8
	Barn Swallow	*Hirundo rustica*	-	4
	Chestnut-backed Chickadee	*Poecile rufescens*	3	-
	Common starling	*Sturnus vulgaris*	5	1
	House Finch	*Haemorhous mexicanus**	6	-
	House Sparrow	*Passer domesticus*	3	-
Other Terrestrial	Hummingbird	Trochilidae	1	-
	Northern Flicker	*Colaptes auratus*	-	1
	Rock Pigeon	*Columba livia*	2	-
Seagull	Glaucous-winged Gull	*Larus glaucescens*	1	5
	Juvenile Gull	*Larus* spp.	1	7
	Ring-billed Gull	*Larus delawarensis*	-	2
	Seagull, unspecified	*Larus* spp.		3
Shore Birds	Spotted Sandpiper	*Actitis macularius*	5	-
Total number of taxa observed			15	12
Total number of observations			110	75

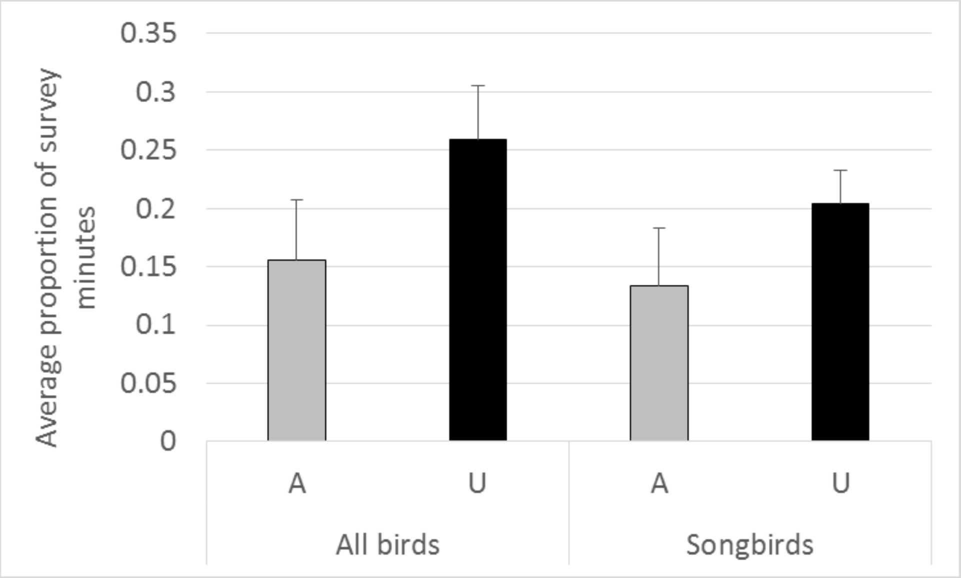

Figure 1 Proportion of survey minutes in which birds were observed on the transect (total minutes of observation/total survey minutes).

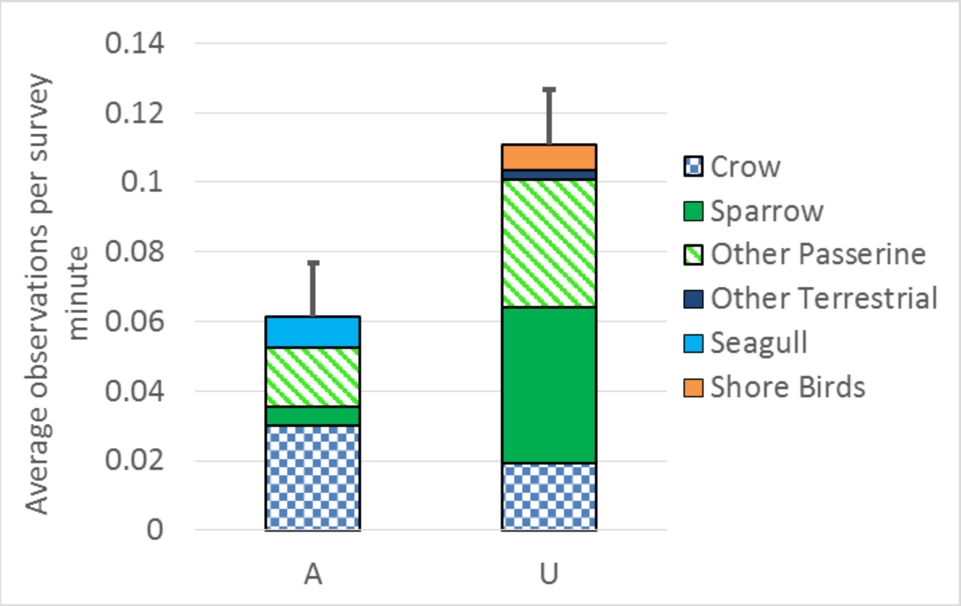

Figure 2 Total number of focal individual observations per survey minute in each taxa group (Table 1) at armored and unarmored beaches.

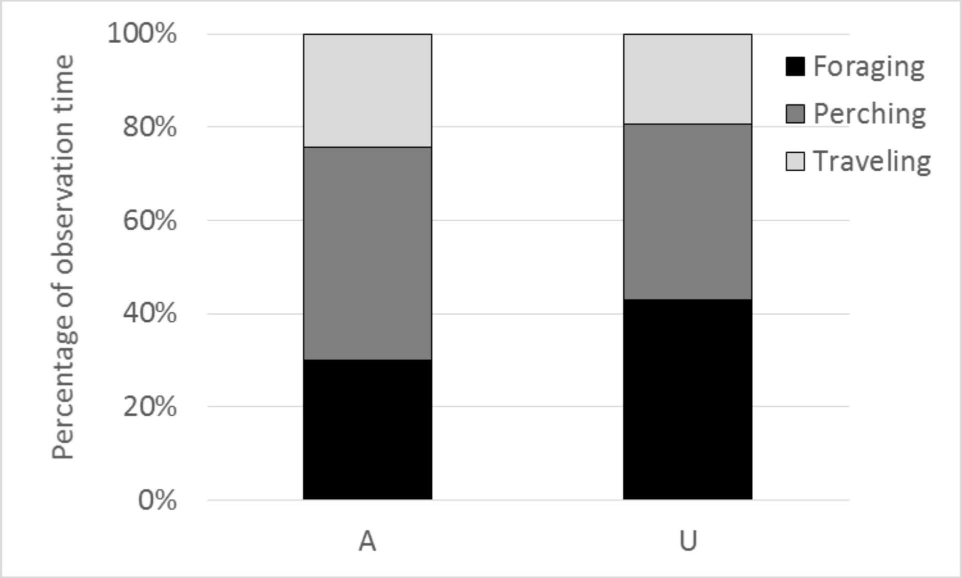

Figure 3 Percentage of time focal birds from all taxa groups were observed in each behavior category at armored and unarmored beaches.

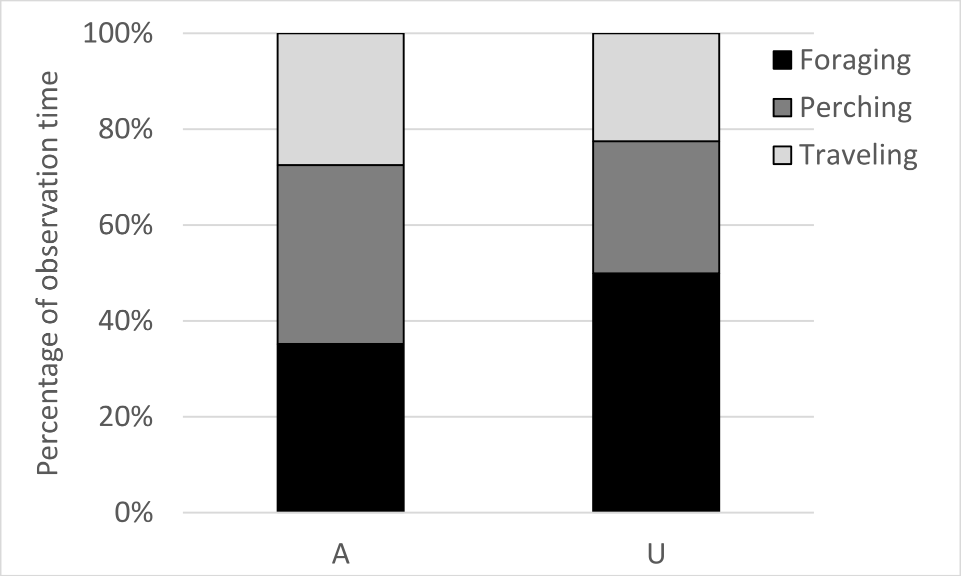

Figure 4 Percentage of time focal terrestrial birds (Corvidae, Emberizidae, Other Passerine, and Other Terrestrial) were observed in each behavior category at armored and unarmored beaches.

References

Altmann, J. 1974. Observational Study of Behavior: Sampling Methods. Behaviour 49: 227-267.

Barrett, K., W.B. Anderson, D.A. Wait, L.L. Grismer, G.A. Polis, and M.D. Rose. 2005. Marine subsidies alter the diet and abundance of insular and coastal lizard populations Oikos 109: 145-153.

Brehme, C.S., W.I. Boarman, S.A. Hathaway, A. Herring, L. Lyren, M. Mendelsohn, K. Pease, M. Rahn, C. Rochester, D. Stokes, G. Turschak, and R.N. Fisher. 2009. Spatial and temporal patterns across an ecological boundary: Allochthonous effects of a young saltwater lake on a desert ecosystem. Journal of Arid Environments 73: 811-820.

Brennan, J.S., and H. Culverwell. 2004. Marine riparian: an assessment of riparian functions in marine ecosystems. Published by Washington Sea Grant Program, Copyright 2005, UW Board of Regents, Seattle, WA. 34 p.

Craik, S.R., J.L. Savard, M.J. Richardson, and R.D. Titman. 2011. Foraging ecology of flightless male Red-breasted Mergansers in the Gulf of St. Lawrence, Canada. Waterbirds 34(3):280-288.

Christie, K.S., M.D. Hocking, and T.E. Reimchen. 2008. Tracing salmon nutrients in riparian food webs: isotopic evidence in a ground-foraging passerine. Canadian Journal of Zoology-Revue Canadienne de Zoologie 86: 1317-1323

Dierschke, V. 1993. Food and feeding ecology of purple sandpipers *Calidris maritima* on rocky intertidal habitats (Helgoland, German Bight). Netherlands Journal of Sea Research 31: 309–317.

Dierschke, J. and F. Bairlein. 2004. Habitat selection of wintering passerines in salt marshes of the German Wadden Sea. Journal of Ornithology 145: 48–58.

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.

Lovvorn, J.R. and J.R. Baldwin. 1996. Intertidal and farmland habitats of ducks in the Puget Sound region: A landscape perspective. Biological Conservation 77: 97–114

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98: 166-170.

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.

Romanuk, T.N. and C.D. Levings. 2010. Reciprocal subsidies and food web pathways leading to Chum salmon fry in a temperate marine-terrestrial ecotone. Plos One 5: e10073.

Sobocinski, K.L., J.R. Cordell and C.A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuaries and Coasts 33: 699-711.

Stapp, P. and G.A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134: 496-504.

Uesugi, A and M. Murakami. 2007. Do seasonally fluctuating aquatic subsidies influence the distribution pattern of birds between riparian and upland forests? Ecological Research 22: 274-281

Withey, J.C. and J.M. Marzluff. 2009. Multi-scale use of lands providing anthropogenic resources by American Crows in an urbanizing landscape. Landscape Ecology 24: 281-293

Wright, A.N., J. Piovia-Scott, D.A. Spiller, G. Takimoto, L.H. Yang and T.W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos 122: 1496-1504.

Chapter 6: Comprehensive conclusion, conceptual model of effects of shoreline armoring on marine-terrestrial linkages in the nearshore ecotone

Introduction

This concluding chapter synthesizes results of all components of my dissertation into a summary conceptual model of the effects of shoreline armoring on marine-terrestrial ecotones. Connections between beach wrack and the primary consumers it supports are addressed; the disruptive effects of armoring on wrack-associated and marine riparian invertebrate assemblages, and consequences for secondary consumers in estuarine and terrestrial ecosystems, are visually illustrated and supported with empirical evidence. The primary approach of this study was comparison of various parameters among pairs of armored and unarmored beaches throughout central and south Puget Sound, with armored shorelines considered as treatments and adjacent unarmored shorelines as references. Physical parameters, wrack, logs, and associated invertebrates were sampled at 29 pairs of beaches over the course of three years, providing broad spatial replication. Juvenile salmon and birds were surveyed at fewer sites but still retained the armored-unarmored pairing aspect that allowed for direct comparison of behavior, feeding rates, and habitat use by shore type.

Primary results

In Chapter Two, I demonstrated that armoring significantly alters the physical and biotic features of the nearshore ecotone as well as connectivity between marine and terrestrial ecosystems. Armored beaches had significantly lower maximum elevations (mean difference 0.9 m; maximum 3.5 m) than unarmored beaches and narrower width (mean difference 8.9 m), inferring an overall reduction in the size of the ecotone. Armored beaches had a greater proportion of cobbles in wrack line sediments, and at the two beach pairs where wave gauges were deployed (included in the larger project but not written into my dissertation), there was an increase in wave heights at armored beaches (Ogston et al., in prep). These physical differences are likely to influence the type and amount of wrack accumulation as well as the diversity and abundance of organisms that can inhabit upper beach sediments. Shoreline armoring reduced the amount of physical space available for deposition and accumulation of wrack and logs, referred to as 'placement loss' (Coyle and Dethier 2010). Sediment grain size and local wave conditions have also been shown to influence the amount and type of wrack deposited on shore (Orr et al. 2005; Barreiro et al. 2011; Gomez et al. 2012), and I found evidence of an influence of sediment size as well, with cobbles in upper beach sediments associated with lower wrack abundance. Further research is needed to determine whether increased local wave heights play a role in the reduced amount of wrack at armored beaches in the nearshore ecotone.

Biotic habitat attributes differed between armored and unarmored beaches, with the former having fewer logs, less wrack overall, and a lower proportion of terrestrial material in both units of percent cover and biomass. These differences mean that armored beaches have significantly less biotic habitat for consumers, and when biotic attributes do exist on armored beaches they are altered relative to unarmored beaches, as evidenced by the significant difference in the types of wrack. I showed that, when it borders marine shores, riparian vegetation is an important source of wrack to natural beaches. When armoring disrupts the connectivity between marine and terrestrial ecosystems, the riparian contribution to beach wrack is greatly reduced in addition to the total amount of wrack. Reciprocal subsidies between systems of similar productivity have been shown to occur across forest-stream ecotones (Nakano and Murakami 2001; Baxter et al. 2005). Recent research has suggested that reciprocal subsidization between forests and marine shorelines also occurs (Paetzoldt et al. 2008; Romanuk and Levings 2010). In Chapter Two, I added evidence that the contribution of terrestrial plant material to beach wrack is widespread among beaches fringed with riparian vegetation and that the potential exists for reciprocal subsidization between marine and terrestrial ecosystems when connections are intact.

Chapter Three focused on invertebrate assemblages of the nearshore ecotone. I demonstrated that armored beaches had significantly different macroinvertebrate assemblages than unarmored beaches, including fewer talitrid amphipods, fewer insects and collembolans, and more aquatic invertebrates. Perhaps most significant was the difference in talitrid amphipods, which are important consumers and decomposers, which were 8.5 times more abundant in wrack at unarmored than at armored beaches. Differences in armored-unarmored wrack invertebrate assemblages were correlated with a variety of environmental variables, including sediment grain sizes, amount and type of wrack and logs, and beach characteristics that define the size of the ecotone (elevation, width). Evidence from experimental tubes installed at unarmored sites that were filled with weighed wrack indicated that these invertebrates play a key role in wrack decomposition, which was significantly faster in tubes with coarse mesh, and were colonized by more talitrid amphipods, insects, collembolans and total invertebrates than tubes with fine mesh. Decomposition was positively correlated with oligochaete and talitrid densities, providing evidence that talitrid amphipods, and likely other wrack-associated macroinvertebrates, play an important role in decomposition and nutrient recycling of the marine and riparian wrack that accumulates in the nearshore ecotone, as has been previously demonstrated in other beach ecosystems (Griffiths and Stenton-Dozey 1981; Mews et al. 2006; Lastra et al. 2008). Invertebrates that consume beach wrack are in turn consumed by other organisms and thus represent a transfer of nutrients to higher trophic levels. Interestingly, the destruction of many of our wrack tubes at armored sites – 42% were lost or broken at armored compared with 18% at unarmored beaches – lent support to the increase in wave energy found in wave gauge studies. Wrack tubes at armored beaches of all elevations experienced a surprising amount of destruction, suggesting that this was not simply an effect of the elevation of armor and associated inundation time and frequency. Pitfall traps that quantified mobile invertebrate abundances around high (usually around +3.66 m MLLW and covered by armoring structures at armored beaches) and low wrack lines (usually around +2.44 m MLLW and often present on both armored and unarmored beaches within a pair) showed no differences among elevations in total invertebrates captured, but there were significant differences in total densities as well as overall assemblages between armored and unarmored beaches. Insects captured in pitfall traps varied both by armoring and by elevation, with greater densities in high compared to low samples, and in unarmored compared to armored samples. The assemblage composition and abundance of these macroinvertebrates are particularly affected by disrupted connectivity in the upper intertidal and/or removal of riparian vegetation. As shown for the amount of beach wrack and number of logs in the previous chapter, the relative abundance of wrack-associated macroinvertebrates are greatly reduced at armored beaches and the potential for effects on higher trophic levels caused by armoring is apparent.

In Chapter Four, I showed that the greatest potential effect of armoring on juvenile salmon is the likely reduction in prey availability caused by the severed riparian connection and the loss of beach wrack and the invertebrate fauna it supports. Snorkel observations found juvenile salmon less frequently and in deeper water at armored beaches at high tide. This suggests that there may be some behavioral response to conditions associated with armoring that makes fish less obvious to snorkelers (e.g. actively foraging fish may be easier to detect by snorkel observation than fish rapidly swimming along a straight-line path through a site) or reduces the proportion of time along armored shorelines (e.g. foraging behavior and path sinuosity may increase the relative amount of time spent along a given stretch of shoreline). The altered depth distribution may influence the types of prey available to juvenile salmon during high tide, when fish along unarmored beaches would be able to forage in shallow water in close proximity to riparian vegetation and other sources of terrestrial insects (e.g. beach wrack and logs) while fish along armored shorelines would have to forage in deeper water (when armoring encroaches on the intertidal zone) in close proximity to armoring structures. I did not find any significant differences in movement rates, proportion of time feeding, or feeding rates by presence or absence of armoring, thus conclude that foraging effort is relatively consistent in the nearshore, although it may be concentrated in certain habitat types over others, i.e. if juvenile salmon spend more time along unarmored shorelines, then they also feed more often in these habitats. Feeding behaviors influenced movement paths and resulted in significantly lower straightness indexes which should result in higher residence times for feeding fish. In general, juvenile salmon showed greater variation in straightness index and movement rates at unarmored beaches, particularly with lower minimum values for those parameters, suggesting that unarmored shorelines accommodate (i.e. provide opportunity for) a greater diversity of behaviors. The lack of significant differences in these parameters may be due to uneven sample sizes based on fishes that could be observed, which necessitated non-parametric comparisons rather than the intended paired t-tests and may have reduced our ability to detect differences. Chapter Three added to the body of research suggesting that armoring reduces riparian insect prey available for juvenile salmon to consume (Romanuk and Levings 2003; Sobocinski et al. 2010). Because juvenile salmon appear to forage at similar rates at both armored and unarmored shorelines, differences in prey availability or prey quality are mechanisms by which armoring represents a reduction in habitat quality. Previous research has shown that salmon survival is related to growth during early marine residency (Duffy and Beauchamp 2011) and may be influenced by estuarine rearing conditions (Magnusson and Hilborn 2003; Greene et al. 2005; Simmons et al. 2013); my results pose a potential mechanism for the effect of estuarine modification on juvenile salmon performance.

In Chapter Five, I demonstrated that the nearshore ecotone provides foraging habitat for terrestrial songbirds and that armoring disrupts this function. Both proportion of survey minutes and number of birds per survey minute (metrics of bird abundance) showed that songbirds were much more common at unarmored beaches. Overall, bird assemblages shifted toward more crows and gulls and fewer songbirds at armored beaches. Songbird abundances were likely reduced at armored beaches due to a combination of factors: (1) the lack of riparian fringe reduces accessibility and refuge habitats; (2) biogenic habitats (such as driftwood logs and riparian vegetation) are preferred because they provide more cover and more food; (3) fewer wrack-associated and riparian invertebrate prey provide limited foraging benefits. All bird taxa observed spent more time perching at armored beaches and feeding at unarmored beaches, indicating a difference in habitat functions; songbirds showed greater magnitude of this difference in behaviors. The proportion of time birds spent foraging and the prey resources available were significantly impacted by shoreline armoring. Perching behaviors were altered as well. Perching birds used logs or riparian vegetation at unarmored beaches, compared to beach substrates or armoring structures at armored beaches. Effects of armoring on terrestrial birds in the nearshore ecotone are behavioral (reduced time spent foraging), trophic (reduced food availability), and structural (altered habitat type; less habitat space; lost connectivity). The sum of these effects may be significant for some populations, and this is the first study to my knowledge documenting the use of wrack zones as habitat for terrestrial birds.

Conceptual model

Investigation of invertebrates, juvenile salmon, and birds in the nearshore ecotone along barrier beaches of Puget Sound shows that beach wrack from terrestrial and marine sources subsidizes riparian and intertidal primary consumers, which in turn potentially subsidize secondary consumers in terrestrial (songbirds) and marine (juvenile salmon) ecosystems. The importance of beach wrack in the nearshore ecotone for talitrid amphipods and insects has been clearly demonstrated in this study, and evidence for subsidization of juvenile salmon and songbirds has been presented. The following conceptual model (Fig. 1) provides a visual synthesis of key results from my dissertation and the links among them. Overall, the effects of armoring in the nearshore ecotone demonstrated in this study are:

- reduced *size* of the ecotone (indicated by overlap of spheres)
- altered *permeability* (i.e. the connectivity between ecosystems, indicated by narrower arrows and red X's);
- reduced amount and altered composition of biogenic habitat for invertebrates and birds (indicated by reduction or loss of black arrows);
- reduced amount and altered food sources for primary consumers (indicated by the narrower and wider white arrows linking leaf litter and algae, respectively, to beach wrack and the narrower yellow arrow linking beach wrack to wrack invertebrates);
- reduced prey for secondary consumers (indicated by the narrower yellow arrows linking wrack invertebrates and riparian insects to birds and juvenile salmon);
- reduced amount and altered type of habitat space for invertebrates, birds, and fish, such as narrower shallow water space (indicated by the “X” over shallow water); coarser wrack line sediments (not illustrated); altered wave climate (not illustrated); upper intertidal logs and

unconsolidated sediments replaced with vertical concrete or riprap (indicated by the "X" over the arrow connecting driftwood and logs); severed marine riparian connection (indicated by the "X" over the arrow linking marine riparian to leaf litter); and,

- reduced temperature regulation of upper beach sediments and microclimate (indicated by the red "X" over temperature regulation).

Uncertainties represented in the conceptual model exist in terms of whether beach wrack and its associated invertebrates constitute a subsidy in the sense of increasing consumer density for songbirds and juvenile salmon, i.e. whether or not a numerical response is produced (Sabo and Power 2002). These secondary consumers are highly mobile and may forage opportunistically, taking advantage of available wrack invertebrates when possible and moving to other habitats when prey are scarce. Sabo and Power (2002) showed that mobile consumers migrate to particular habitat patches within and across ecotones according to the distribution of prey resources; I found evidence that this may occur for juvenile salmon and terrestrial birds in the nearshore ecotone that were more often observed along unarmored shorelines, where higher abundances of arthropods and crustaceans occurred. The relative importance of prey derived from beach wrack in terms of productivity for juvenile salmon (terrestrial arthropods including dipteran flies, hemipterans, and collembolans) and songbirds has yet to be quantified. Our results indicate that the potential for subsidization of secondary consumers exists given the high abundances of prey organisms associated with beach wrack (and lacking when that wrack is absent due to armoring), the higher frequency of occurrence (i.e. more observations at unarmored beaches despite equal sampling effort) of juvenile salmon along unarmored shorelines and their consistently high rates of foraging, and the higher proportion of time that songbirds spend foraging among wrack at unarmored beaches. An additional uncertainty is whether reduced shallow water habitat space negatively affects juvenile salmon, for example by increasing predation risk or energetic costs. Snorkel surveys presented in Chapter 4 were conducted during high tide, when the narrowed beach width and steeper depth gradient associated with armoring would have the greatest effect. However, juvenile salmon are highly mobile and may simply avoid or minimize time spent along deeper armored habitats in favor of shallower natural habitats, thereby minimizing the effects of armoring. Avoidance behaviors, such as increased movement rates and/or reduced time devoted to feeding behaviors when swimming past armored shoreline habitats would come with energetic costs that may or may not be compensated when fish reach more favorable unarmored habitats.

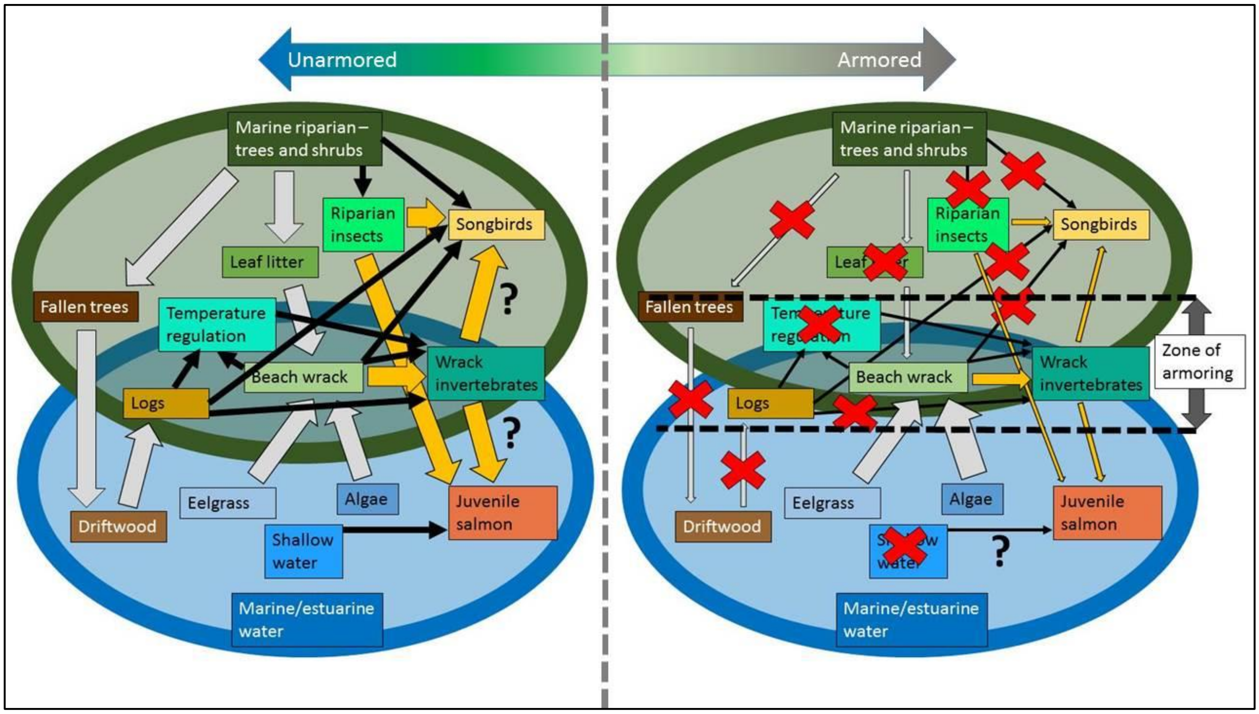

Figure 1 Conceptual model of biological effects of armoring on nearshore ecotone linkages. Direction of arrows indicates source to recipient. Width of the arrows represents strength of the linkage. Severed linkages are indicated by a red "X" and uncertainties are represented by "?" Yellow arrows are trophic linkages, white arrows are inputs of organic material, black arrows represent habitat linkages. The size of the overlap between marine riparian and marine/estuarine water spheres represents the size of the ecotone.

Questions for future research

Physical variables

Armored beaches in this study had a higher proportion of cobble in wrack line sediments compared to unarmored beaches. Investigation of the physical mechanisms driving this pattern would contribute to better understanding of the physical responses of different beach types to armoring. Wave energy differences resulting from reflection off of armoring structures or differences in beach hydrology resulting from differences in permeability of armored and unarmored substrates are two examples of physical mechanisms that could influence sediment distribution. In this study, differences in wave heights were detected at the two armored-unarmored pairs where wave gauges were deployed. Further research is needed to determine if this is a consistent effect of shoreline armoring for mixed-sediment, fetch-limited beaches like those in Puget Sound, as well as other beach types.

Wrack and logs

Identifying the broader scale of impact of reduced beach wrack on armored beaches, i.e., whether consequences are limited to local effects in the upper intertidal where armoring occurs, or extend to larger-scale issues like or nearshore nutrients and productivity. On sandy beaches, Dugan et al. (2011) found dissolved organic and dissolved inorganic nitrogen concentrations in intertidal pore water and in nearshore surf zone water to be correlated with the biomass of beach wrack, indicating that the breakdown of beach wrack is an important source of nutrients to beach sediments and nearshore waters.

Previous research showed greater wrack deposition among cobble sediments because of the larger pore spaces effectively trapping wrack pieces (Orr et al. 2005). However, results presented in Chapter 2 (Heerhartz et al., in press) indicated more wrack (as well as unarmored beaches in general) associated with pebble and gravel and less wrack (as well as armored beaches) associated with sand and cobble, thus the role of sediment size and site-specific swash zone processes in wrack deposition is unclear. Further research is needed to determine what physical mechanisms link wrack abundance and composition to sediment characteristics on different beach types.

All of the unarmored beaches in this study, the lowest of which had a toe elevation of 2.91 m, had logs in the upper intertidal; for armored beaches with toe elevation above 3.5 m, 6 of 8 had a few logs, compared to 3 of 21 armored beaches with toe elevations of 3.5 m or less having any logs. Whether or not this represents some sort of threshold elevation, particularly in the context of the tidal frame and occurrence of wave action and inundation needs investigation.

Wrack invertebrates

In the nearshore ecotone, the amount and type of beach wrack is correlated with abundance and species composition of supralittoral invertebrate communities. Further research is needed to understand the mechanisms for these correlations and the importance of different sources (terrestrial plants, algae, eelgrass) of beach wrack as habitat for invertebrates including talitrid amphipods and insects. Within the wrack community, terrestrial, algal, and eelgrass components of wrack may serve different functions (e.g. food, refuge) for different primary consumers and identification of trophic pathways leading to high invertebrate densities is important for understanding the ecology of these systems. Studies from sandy beaches have shown that a variety of secondary consumers prey upon invertebrates associated with beach wrack (Dugan et al. 2003; Stapp and Polis 2003; Lewis et al. 2007; Wright et al. 2013). I observed songbirds and other terrestrial birds consuming insects and talitrid amphipods among beach wrack and logs; future work could identify other organisms utilizing wrack prey resources in nearshore ecotones.

The armored beach where sediment temperatures were recorded over a three-month period (May – July) showed dramatic increases in temperature during the day when exposed, while the temperatures at the same elevation as well as the maximum elevation on its companion unarmored beach remained consistent. Overall, average sediment temperatures were higher at the armored beaches, consistent with what Rice (2006) found for a pair of beaches in northern Puget Sound over the course of 4 summer days. The armored beach in that study had reduced environmental buffering compared to the unarmored beach for a number of variables, resulting in higher average daytime light intensity, higher average air and sediment temperatures, and lower humidity. These differences were linked to reduced survival of surf smelt eggs, but such differences in microclimate likely influence supralittoral invertebrates inhabiting beach sediments and wrack and may explain some of the differences found in invertebrate abundance and community composition. Further work to investigate the ecological role of microclimate alteration resulting from shoreline armoring would add to our knowledge of abiotic factors affecting beach wrack invertebrate communities.

Forage fish

Some forage fish species, such as surf smelt (*Hypomesus pretiosus*) and Pacific sand lance (*Ammodytes hexapterus*), rely on upper intertidal beaches for spawning habitat. Previous research has indicated that shoreline armoring negatively affects the survival of surf smelt eggs (Rice 2006). That study was conducted at a single armored-unarmored beach pair over a relatively short time period (4 days) in northern Puget Sound. I originally proposed to investigate whether the effect of shoreline armoring on forage fish eggs is a consistent pattern throughout Puget Sound that acts on both surf smelt and sand lance. However due to constraints of time and the multiple other facets of my dissertation research I was unable to address effects of armoring on forage fish. This is an important area for future research for all species of obligate beach-spawning forage fish that serve as trophic linkages in marine and estuarine food webs. If the pattern of increased embryo mortality on armored beaches demonstrated by Rice (2006) is consistent for different forage fish species and other nearshore systems, population-level declines in these species could result from increases in shoreline armoring.

Future research should seek to understand the mechanism for spawning site selection by surf smelt and sand lance and whether armoring reduces the reproductive success of beach spawning forage fish on an estuary-wide scale because of the negative effects on egg survival, or whether forage fish are able to select and utilize adequate unarmored beach space. Shoreline armoring reduces the overall amount of spawning substrates by encroaching on the upper intertidal, but if surf smelt and sand lance use ~10% of the shoreline of Puget Sound for spawning (Penttila 2007), then suitable unarmored sites may not be a limiting factor. Juvenile and adult forage fish are consumed by many marine and estuarine organsims, but less is known about potential consumers of beach-spawning forage fish eggs. Diving birds have been shown to consume herring eggs attached to eelgrass; and shorebirds consume beach-spawning horseshoe crab eggs (Nordstrom et al. 2006). Organisms that forage in beach wrack and among upper beach sediments may consume surf smelt or sand lance eggs when present; future research should investigate whether any consumers rely on forage fish eggs as a seasonal resource, which may also be affected by shoreline armoring.

Juvenile salmon

Terrestrial insects have been shown to be an important prey source for juvenile salmon in shallow nearshore waters; these insects likely come from riparian vegetation close to shore (Romanuk and Levings 2003), but beach wrack may also be a source of terrestrial insects (Chapter 3). Whether or not any of the insects that inhabit beach wrack are preyed upon by juvenile salmon remains to be investigated, although many of the invertebrate taxa found in beach wrack samples have been reported in diets of chum salmon in the nearshore ecotone of Howe Sound, British Columbia (Romanuk and Levings 2010). Shoreline armoring often involves removal or alteration of both riparian vegetation and beach wrack and thus may reduce the amount of insect prey available for juvenile salmon. Terrestrial insect subsidies to fishes (including juvenile salmon) in lakes are negatively correlated with shoreline development and removal of riparian vegetation (Francis and Schindler 2009). Future studies should test for differences in neuston (insects and other organisms floating on the surface of the water) abundance and composition along armored and unarmored shorelines to determine whether there is a local effect of armoring on terrestrial insect subsidies and prey availability for juvenile salmon in the nearshore ecotone.

I observed juvenile salmon feeding primarily at the surface of the water and quantified their feeding rates (number of prey attacks per minute) and identified types of insects and other arthropods associated with beach wrack on armored and unarmored beaches. This information combined with future research on the amount and type of neuston available along armored and unarmored shorelines could shed light on aquatic-terrestrial linkages across the nearshore ecotone, specifically whether beach wrack invertebrates (e.g. insects and other arthropods) can become available as prey for juvenile salmon and whether shoreline armoring affects juvenile salmon growth and survival.

Terrestrial birds

Birds have been shown to utilize aquatic resources in many aquatic-terrestrial ecotones (Lovvorn and Baldwin 1996; Polis and Hurd 1996; Nakano and Murakami 2001; Dugan et al. 2003; Brehme et al 2009). However few studies have investigated bird use of nearshore ecotone habitats, specifically whether beach wrack in these systems subsidizes birds as it does in sandy coastal systems. My research highlighted a number of questions and opportunities for research on bird use of nearshore ecotones. I showed that terrestrial birds forage in beach wrack and among logs, and that different species use armored and unarmored beach habitats. Further research is needed to determine whether beach wrack actually represents a subsidy for terrestrial birds (e.g. if it increases their abundances relative to adjacent terrestrial habitats), or whether the nearshore ecotone represents an opportunistic foraging habitat. The importance of beach wrack and logs for bird likely varies by species and season, and for resident and migratory birds. Nearshore ecotones may provide habitat functions beyond foraging, such as nesting and predator refuge; future research could identify bird use of specific ecosystem components (e.g. logs, wrack, riparian vegetation) for different habitat functions.

Conservation and restoration implications

This study adds to the growing body of evidence that reciprocal subsidies are important along many different types of aquatic-terrestrial ecotones, and specifically that beach wrack subsidies are important in other types of coastal systems in addition to wave-exposed sandy beaches where most beach wrack studies have focused. Changes to ecosystem connectivity have consequences for the connected (or disconnected) systems, and connectivity across ecotones need to be considered for conservation and restoration of functional ecosystems. This type of "cross-ecosystem" thinking is needed to develop adequate shoreline management policies that can effectively predict effects of armoring in specific scenarios and identify priorities for restoration and conservation. In the case of juvenile Chinook salmon in Puget Sound, our results indicate that maintaining or restoring production and availability of invertebrate prey (e.g., by prioritizing marine-terrestrial connectivity) could reduce some of the effects of shoreline armoring.

Local studies have shown that removal of shoreline armoring restores wrack deposition and natural log recruitment (Toft et al. 2010). At Seahurst Park, this restoration facilitated re-development of wrack invertebrate communities (particularly talitrid amphipods), while at the Olympic Sculpture Park (OSP) in a highly urbanized setting, talitrid amphipods did not establish during the first three years following construction of the pocket beach despite recruitment of wrack and logs to the upper beach. In the case of OSP, the lack of development of invertebrate communities that normally accompany wrack and logs could have been related to the lack of any nearby source populations, since all of the surrounding shoreline remains armored. The physical characteristics of the beach may also play a role in this case; the OSP pocket beach has coarser sediments and a steeper slope than natural beaches in Puget Sound, features which may influence the moisture retention of sediments or other characteristics that determine inhabitability for talitrid amphipods. Restoration of marine-terrestrial connectivity and/or wrack and log deposition may not result immediately in the return to an intact nearshore ecotone, but it does provide the potential for linkages to return over time. Further studies such as this, that attempt to understand relationships between physical and biological variables and connections between adjacent ecosystems are critical to effective nearshore restoration and conservation efforts. This type of information might be most important for novel ecosystems that are created when natural environments are modified by anthropogenic activity, where restoration or rehabilitation efforts within urban constraints may be limited to a few key habitat functions or ecosystem connections. Basing the decision of which functions, attributes, or connections to restore on ecological data such as those presented here will give the best chance for successful restoration or habitat enhancement projects in anthropogenically modified ecosystems.

References

Barreiro, F., M. Gomez, M. Lastra, J. Lopez, and R. de la Huz. 2011. Annual cycle of wrack supply to sandy beaches: effect of the physical environment. Marine Ecology Progress Series 433: 65-74.

Baxter, C.V., K.D. Fausch, and W.C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology 50: 201-220.

Brehme, C.S., W.I. Boarman, S.A. Hathaway, A. Herring, L. Lyren, M. Mendelsohn, K. Pease, M. Rahn, C. Rochester, D. Stokes, G. Turschak, and R.N. Fisher. 2009. Spatial and temporal patterns across an ecological boundary: Allochthonous effects of a young saltwater lake on a desert ecosystem. Journal of Arid Environments 73: 811-820.

Coyle, J.M. and Dethier, M.N. 2010. Review of shoreline armoring literature, *in* Shipman, H., Dethier, M.N., Gelfenbaum, G., Fresh, K.L., and Dinicola, R.S., eds., 2010, Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, pp 245 – 265.

Duffy, E.J. and D.A. Beauchamp. 2011. Rapid growth in the early marine period improves the marine survival of Chinook salmon (*Oncorhynchus tshawytscha*) in Puget Sound, WA. Can J Fish Aquat Sci 68: 232-240.

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.

Dugan, J. E., D.M. Hubbard, H.M. Page, and J.P. Schimel. 2011. Marine macrophyte wrack inputs and dissolved nutrients in beach sands. Estuaries and Coasts 34: 839-850.

Francis, T.B. and D.E. Schindler. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos 118: 1872-1887.

Gomez, M., F. Barreiro, J. Lopez, M. Lastra and R. de la Huz. 2012. Deposition patterns of algal wrack species on estuarine beaches. Aquatic Botany 105: 25-33.

Greene, C.M., D.W. Jensen, G.R. Pess, E.A. Steel, and E. Beamer. 2005. Effects of environmental conditions during stream, estuary, and ocean residency on Chinook salmon return rates in the Skagit River, Washington. Transactions of the American Fisheries Society 134: 1562-1581.

Griffiths, C.L. and J. Stenton-Dozey. 1981. The fauna and rate of degradation of stranded kelp. Estuarine, Coastal and Shelf Science 12: 645-653.

Lastra, M., H.M. Page, J.E. Dugan, D.M. Hubbard, and I.F. Rodil. 2008. Processing of allochthonous macrophyte subsidies by sandy beach consumers: estimates of feeding rates and impacts on food resources. Marine Biology 154: 163-174.

Lewis, T.L., M. Mews, D.E. Jelinski, and M. Zimmer. 2007. Detrital subsidy to the supratidal zone provides feeding habitat for intertidal crabs. Estuaries and Coasts 30: 451-458.

Lovvorn, J.R. and J.R. Baldwin. 1996. Intertidal and farmland habitats of ducks in the Puget Sound region: A landscape perspective. Biological Conservation 77: 97–114

Magnusson, A. and R. Hilborn. 2003. Estuarine influence on survival rates of Coho (*Oncorhynchus kisutch*) and Chinook salmon (*Oncorhynchus tshawytscha*) released from hatcheries on the US Pacific Coast. Estuaries 26: 1094-1103.

Mews, M., M. Zimmer, and D.E. Jelinski. 2006. Species-specific decomposition rates of beach-cast wrack in Barkley Sound, British Columbia, Canada. Marine Ecology Progress Series 328: 155–160.

Nakano, S. and M. Murakami. 2001. Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America 98: 166-170.

Nordstrom, K.F., N.L. Jackson, D.R. Smith, and R.G. Weber. 2006. Transport of horseshoe crab eggs by waves and swash on an estuarine beach: Implications for foraging shorebirds. Estuarine, Coastal and Shelf Science 70: 438–448.

Orr, M., M. Zimmer, D.E. Jelinski, M. Mews. 2005. Wrack deposition on different beach types: Spatial and temporal variation in the pattern of subsidy. Ecology 86: 1496-1507

Paetzold, A., M. Lee, and D.M. Post. 2008. Marine resource flows to terrestrial arthropod predators on a temperate island: the role of subsidies between systems of similar productivity. Oecologia 157: 653–659.

Penttila, D. 2007. Marine forage fishes in Puget Sound. Puget Sound Nearshore Partnership Report No. 2007-03. Published by Seattle District, U.S. Army Corps of Engineers, Seattle, WA.

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.

Rice, C.A. 2006. Effects of shoreline modification on a northern Puget Sound beach: microclimate and embryo mortality in surf smelt (Hypomesus pretiosus). Estuaries and Coasts 29:63-71.

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.

Romanuk, T.N. and C.D. Levings. 2010. Reciprocal subsidies and food web pathways leading to Chum salmon fry in a temperate marine-terrestrial ecotone. Plos One 5: e10073.

Sabo, J.L. and M.E. Power. 2002. Numerical response of lizards to aquatic insects and short-term consequences for terrestrial prey. Ecology 83: 3023-3036.

Simmons, R.K., T.P. Quinn, L.W. Seeb, D.E. Schindler, and R. Hilborn. 2013. Role of estuarine rearing for sockeye salmon in Alaska (USA). Mar Ecol Prog Ser 481: 211-223.

Sobocinski, K.L., J.R. Cordell and C.A. Simenstad. 2010. Effects of shoreline modifications on supratidal macroinvertebrate fauna on Puget Sound, Washington beaches. Estuaries and Coasts 33: 699-711.

Stapp, P. and G.A. Polis. 2003. Marine resources subsidize insular rodent populations in the Gulf of California, Mexico. Oecologia 134: 496-504.

Toft, J.D., J.R. Cordell, S.M. Heerhartz, E.A. Armbrust, and C.A. Simenstad. 2010. Fish and invertebrate response to shoreline armoring and restoration in Puget Sound. In Shipman, H., M.N. Dethier, G. Gelfenbaum, K.L. Fresh, and R.S. Dinicola, eds., 2010, Puget Sound Shorelines and the Impacts of Armoring – Proceedings of a State of the Science Workshop, May 2009: U.S. Geological Survey Scientific Investigations Report 2010-5254, p 161-170.

Toft, J.D., A.S. Ogston, S.M. Heerhartz, J.R. Cordell, and E.E. Flemer. 2013. Ecological response and physical stability of habitat enhancements along an urban armored shoreline. Ecological Engineering 57: 97–108.

Willson, M.F and R.H. Armstrong. 1998. Intertidal foraging for Pacific Sand-Lance, *Ammodytes hexapterus*, by birds. Canadian Field-Naturalist 112: 715-716.

Wright, A.N., J. Piovia-Scott, D.A. Spiller, G. Takimoto, L.H. Yang and T.W. Schoener. 2013. Pulses of marine subsidies amplify reproductive potential of lizards by increasing individual growth rate. Oikos 122: 1496-1504.