

Overview of the Ecology of Puget Sound Beaches

Megan N. Dethier¹

Introduction

As described elsewhere in this Proceedings (Shipman, 2010), shorelines in Puget Sound are diverse in terms of geomorphology and corresponding biotic communities. In marine and estuarine ecosystems, a limited set of physical parameters – substrate type, depth or elevation, and wave or current energy – strongly constrain the distributions of organisms (Dethier, 1990; Kozloff, 1993; Dethier and Schoch, 2005); this linkage is now acknowledged in national systems for classifying marine habitats, which rely in large part on these physical factors (for example, Allee and others, 2000; Madden and others, 2009). In estuaries, patterns of variation in salinity and temperature also contribute to the character of the biota, but because these often co-vary with other physical parameters, it is difficult to tease out critical forcing factors (Dethier and Schoch, 2005). For example, moving from the mouth to the head of an estuary usually involves gradients in sediment type (sand to mud), wave energy (high to low), salinity (marine to fresh, or less variable to more variable), and temperature (usually more stable to less stable). These gradients exist even in deep, well-mixed fjordal estuaries like Puget Sound, although ranges in salinity and temperature are much less than in drowned-river estuaries like the Chesapeake (Dethier and others, 2010). There salinities range from pure fresh to pure marine along the gradient, whereas in Puget Sound salinity seldom drops below 25 practical salinity units (psu) except directly in front of river mouths. As a result of this relative uniformity in water characteristics, the primary factors controlling the ecology of Puget Sound beaches are likely to be substrate type and wave energy, which also co-vary (for example, mud is not found in areas of high waves or currents). The following discussion of the ecology of Puget Sound beaches thus focuses on the plants and animals characteristic of the various beach types, as defined largely by substrate type.

Shoreline Types

The complex coastline of Puget Sound consists of a large proportion of linear, relatively open shorelines plus small to large embayments and several large river deltas. No beaches in the Sound are exposed to oceanic swells, and thus none would be classified as Exposed or High Energy in various classification systems (Dethier, 1990; Washington State Department of Natural Resources, 2001). There is, however, a range of energies from moderately exposed, on beaches open to long north-south wave fetches, to very protected in shallow embayments, such as those common in south Sound. The range of wave and current energies results in a range of unconsolidated sediment types that comprise the beaches, from coarse gravel-cobble to very fine, organic-rich silts.

Several attempts have been made to quantify the relative abundance of different beach-sediment types within the Sound. Figure 1 shows one such effort, derived from the DNR data, based on the simple length of shorelines categorized into particular substrate types (but ignoring the width of the intertidal zone or polygonal areas such as deltas). This system places every shore ‘unit’ into one substrate category, even though a given stretch of shore may have (for example) coarse gravel on the upper shore and fine mud on the lower shore. Another effort (Bailey and others, 1998) used shoreline area rather than length, classifying each polygon (including one zone of a complex beach) into a substrate category. Despite these differences, the data on relative proportions of different substrate types are surprisingly similar. Puget Sound beaches are dominated by pebbles, sand, and mud (fig. 1), commonly in combination; a frequent pattern on beaches open to the Sound is a coarse pebble-sand mix on the upper shore and cleaner sand on the lower shore. Upper-shore communities are discussed separately below; it is at these higher levels where shoreline armoring (hardening with seawalls, riprap, or other solid structures) generally occurs. Larger size sediments and consolidated (rocky) shorelines are uncommon, although an ecologically important beach type (see below) is the mixed-coarse or rock-gravel-sand type that is scattered throughout the Sound. The dearth of bedrock shores and preponderance of erodible beach types leads to the high demand for armoring for shoreline protection. The different beach types vary dramatically in the productivity and diversity of their biota, and in their perceived “value” to humans; these factors are discussed below.

¹University of Washington, Biology Dept. and Friday Harbor Laboratories, Friday Harbor, Washington. 98250, mdethier@u.washington.edu.

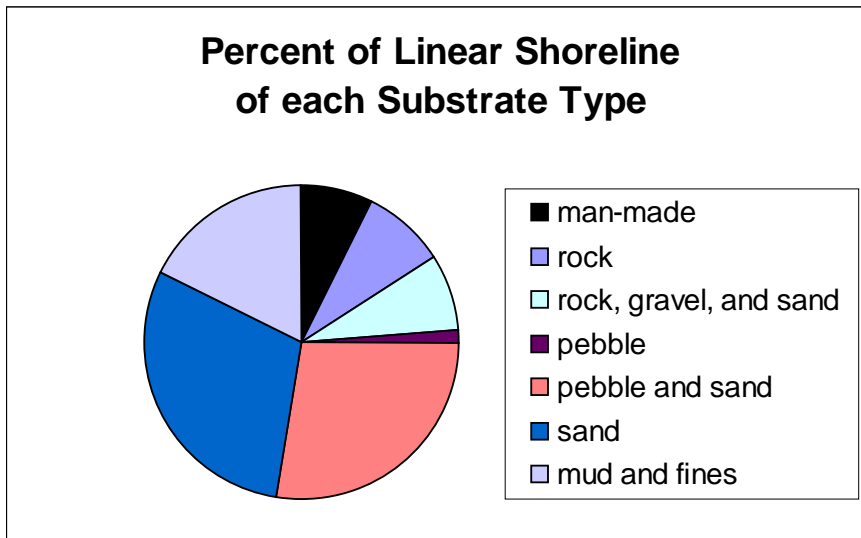


Figure 1. Percent of linear extent of shoreline (not area) in Puget Sound estimated for each substrate type. Substrate types are categorized on the basis of aerial observations and thus do not comprise particular grain sizes. The “rock, sand, gravel” type is similar to the “mixed coarse” in other classifications. From Washington State DNR data, 2001. http://www.dnr.wa.gov/Publications/aqr_nrsh_shrzne_sum_find.pdf.

Biotic Communities

Mud Habitats

The material on muddy beaches in Puget Sound ranges from extremely soft and anoxic muds to firmer sandy mud, sometimes called “mixed fines” (table 1). Primary producers in these habitats consist mostly of benthic diatoms, which sometimes form a thin brown coating on the sediment surface; these are actually highly productive organisms despite their very limited biomass (Thom, 1989; Thom and Albright, 1990). Green algal blades (“ulvoids,” of several species) may be present, either attached to pebbles, bits of shell, or worm tubes, or free-floating; these too are highly productive (Thom, 1984). If dense mats develop in one location, they may kill beach infauna because they prevent feeding and oxygenation of the sediment below them, and rotting mats add a huge biological oxygen demand (Bolam and others, 2000; Auffrey and others, 2004). Eelgrass (*Zostera marina*; see below) is found in sandier areas in the low intertidal zone, although not in bays in southernmost Puget Sound (Washington State Department of Natural Resources, 2001).

Mud shores, as well as mixed-fine shores, are often dominated by burrowing mud shrimp (*Upogebia pugettensis*) or ghost shrimp (*Neotrypaea californiensis*), which aerate but further soften the sediment with their extensive burrow systems (Dumbauld and Wyllie-Echeverria, 2003). Some broad muddy tide flats in protected coves have thousands of characteristic mounds from these species. Other common occupants of mud are deposit-feeding clams (especially *Macoma nasuta* and *M. balthica*), some polychaetes

(especially spionids and capitellids), and amphipod crustaceans (especially corophiids). Until the early 1900s, many muddy shores in Puget Sound, especially in southern bays, had dense populations of the Olympia oyster, *Ostrea conchaphila*; however, a combination of overharvesting, pollution, and introduced predators reduced their populations to very small levels (McKernan and others, 1949). Another commercial shellfish species, the geoduck clam *Panopea generosa*, can be found very low on muddy shores but it is more common in higher-energy and subtidal habitats (Dethier, 2006).

Mixed-Fine Habitats

Many open shorelines in Puget Sound have mid-low shore areas characterized by a mix of sand and mud, often referred to as “mixed-fines.” This substrate may be optimal for eelgrass (Mumford, 2007), both the native *Zostera marina* and the introduced *Z. japonica*. The native eelgrass lives low on the shore and in the shallow subtidal zone, while the Asian species tends to inhabit slightly higher zones. Both are highly productive species that also stabilize the substrate, and create refuge habitat and feeding grounds for juvenile fishes, crabs, and other species (reviewed in Mumford, 2007). They are critical habitat for juvenile salmon migrating along the shoreline. Co-occurring with eelgrass, or in areas between eelgrass patches, are a variety of infaunal species characteristic of either mud and sand habitats, such as amphipods, *Macoma* clams, horse clams (*Tresus* spp.), geoducks, burrowing sea cucumbers and anemones, and a variety of tube-building and mobile polychaete worms.

Table 1. Summary of key ecological features of different shoreline habitats in Puget Sound.

[Species richness data come from identical 50-m transects at different areas around the Puget Sound (Dethier and Schoch, 2005; Dethier and Berry, 2009). N.D., not determined]

Habitat	Primary producers	Dominant species	Species richness	“Valued” species
Mud and mixed-fine sediments	Diatoms, ulvoids, eelgrass	Ghost and mud shrimp, bent-nose clams, polychaete worms, amphipods	15–30	Olympia oysters, shorebirds, geoduck clams, juvenile salmon, Great Blue Heron
Sand	Very few, sometimes eelgrass	Sand dollars, cockles, horse clams, polychaetes	5–25	Shorebirds, geoduck clams, human recreation
Mixed-coarse	Green, red and brown macroalgae including some kelps	Ulvoids, barnacles, anemones, crabs, snails, clams, seastars, polychaetes	25–75	Hardshell clams, Cancer crabs, Pacific oysters
Bedrock or Artificial	Green, red and brown macroalgae including some kelps	Rockweed, ulvoids, mussels, barnacles, snails, seastars	N.D.	Some shorebirds, Pacific oysters
High-Shore (sand and pebbles)	Very few intrinsic	Amphipods, isopods	N.D.	Forage fish (spawning), juvenile salmon (feeding), shorebirds, human recreation

Sand Habitats

Moderate-energy, open sand beaches and embayments often have extensive eelgrass beds; only in the areas of greatest wave fetch does the substrate become too unstable for eelgrass to remain rooted. Certain beaches in Puget Sound without eelgrass have beds of sand dollars (*Dendraster excentricus*), which live primarily subtidally but extend up into the low or even mid-shore. When present, they tend to be very dense (reaching densities of $>1,000/m^2$) and exclude other biota via bioturbation (Schoch and Dethier, 1997). The relative instability of the sediment in these higher-energy beaches reduces the density and diversity of occupants. Beaches without eelgrass or sand dollars have sparse clam populations (including *Macoma secta*, horse clams and *Clinocardium* cockles), and a different array of sparse polychaete species than in mud. Commercially valuable geoduck clams can be found naturally or cultured on sandy shorelines. Upper shore areas, as in mixed-fine habitats, tend to be composed of depauperate steep gravel-sand sediments.

Mixed-Coarse Habitats

In areas where cobbles ($>\sim 10$ cm diam.) are abundant on the low shore, the substrate is stabilized into a complex mix of cobbles, pebbles, and sand; these habitats harbor a rich flora (on the cobbles) and fauna (both on the cobbles and infauna) (Dethier and Schoch, 2005). These are by far the richest intertidal habitats in Puget Sound, and probably have the highest primary and secondary productivity (table 1). Ulvoid algae often cover the cobbles, especially in the summer, and there are smaller amounts of diverse red, brown, and additional green algae. In areas rarely uncovered by the tide, large amounts of kelp (as well as the invasive brown alga *Sargassum muticum*) are present. Animals living attached to or hiding under the cobbles include barnacles, anemones, crabs (including recreationally important *Cancer* spp.) and smaller crustaceans, and snails of many types. The infauna living in the sediment beneath the cobbles is likewise diverse, with many more species and higher biomass than in sand or mud habitats. These include a wide diversity of polychaetes and other worms, small crustaceans, and other invertebrates.

Recreationally and commercially harvested clam species are abundant; these include hardshell clams such as littlenecks (*Protothaca* spp. and *Venerupis*), butter clams (*Saxidomus* spp.), and others (for example, *Macoma inquinata*, cockles). Predators on these clams include seastars, moon snails, dogwhelks, Cancer crabs, marine birds, and humans. While most of these clam species can be found in other habitats, they reach highest abundances in this mixed sediment, probably because individuals of all sizes are hard for predators and wave energy to reach; digging in the substrate is difficult, even for humans with shovels. The importance of cobble for successful survival of these clams was found long ago, when beach owners and aquaculturists began adding gravel or cobble to sandy beaches to enhance clam abundance and growth (Glude, 1978; Schink and others, 1983; Thom and others, 1994). In some areas, for example throughout Hood Canal, introduced Pacific oysters (*Crassostrea gigas*) are common on the mid and low shore, attached to cobbles or to each other.

Bedrock Habitats

Bedrock shorelines are quite uncommon in the Sound proper (fig. 1), although they dominate the shore in the San Juan Islands. Artificial “shorelines”, such as riprap around marinas, may contain similar biota to bedrock shores (Pister, 2009), although these similarities have not been studied in Puget Sound. Patches of hardpan (resistant basal till) are present on some beaches, but their biota has not been surveyed extensively. In general, the plants and animals seen on these hard substrates are an estuarine-tolerant subset of those seen on more-marine shores such as in the San Juans. *Fucus* (brown rockweed) is the dominant primary producer. Other common species include barnacles, blue mussels (*Mytilus trossulus*), various small snails and limpets, small crabs, chitons, and seastars. Areas where silt settles on the rock have even lower diversity.

High-Shore Habitats

Although mid- and low-shore beach substrates and biota vary widely around Puget Sound, the upper-shore areas of many beach types are similar; frequently, beaches that have sand, cobble, or even mud in the low shore have very different sediment at higher elevations. Mid-shore beaches tend to be steeper and often coarser than the low shore, characterized by pebbles, small cobbles, and sand. They are physically unstable and biologically relatively depauperate in marine species, with sparse populations of worms and small crustaceans (amphipods and isopods). At the highest shore level, however, the beach is often less steep and more stable, creating a zone that fills several key ecological functions (Rice, 2010; Toft and others, 2010). Areas at or above Ordinary High Water are

often either sandy or have sand mixed with pebbles, and are the site of accumulation of driftwood and detritus from both terrestrial and marine sources. They can be densely occupied by talitrid (“beach hopper”) amphipods, which are important decomposers and are prey for some shorebirds (Dugan and others, 2008). This is also the habitat used for spawning by several species of forage fishes that are central to Puget Sound food webs (especially surf smelt (*Hypomesus pretiosus*) and sand lance (*Ammodytes hexapterus*): see Penttila, 2007 and Rice, 2010). However, this supratidal zone is often covered by armoring, which effectively eliminates all these ecological functions unless it is built well above the zone of the highest high tides.

Marsh Habitats

Marshes in Puget Sound range from areas encompassing many square miles of vegetation (for example, rushes, sedges, grasses) on the large river deltas to narrow strips of marsh plants (for example, pickleweed *Salicornia*) in the supratidal zone of low-energy linear beaches (usually those without armoring, although found sometimes in front of high-shore seawalls). Characteristic marsh types are controlled by substrate and wave energy, as with the communities described above, but also by degree of freshwater influence from rivers or streams. Diagnostic marsh species and associates for marsh types found in Puget Sound are described in Dethier (1990). The human modifications most often seen in marsh habitats are not armoring, as with the other habitats described above, but diking and filling. They will not be discussed further here.

Links to Other Ecosystem Components

Puget Sound beaches are very much “in the middle” of nearshore ecosystems, with organisms and processes on the shore providing key linkages between terrestrial and marine food webs (see Toft and others, 2010). At low tide, a variety of birds use the beaches, include Great Blue Herons (*Ardea herodias*), gulls, Dunlin (*Calidris alpina*), and other shorebirds; they feed, roost, and in some cases nest there (reviewed in Buchanan, 2006; Eissinger, 2007). At high tide, species such as cormorants (*Phalacrocorax* spp.), grebes (numerous species), mergansers (*Mergus* spp.), and scoters (*Melanitta* spp.) feed near shore. On unaltered shorelines, overhanging vegetation links to the marine realm by dropping both detritus and insects onto the shore (Brennan, 2007). This detritus (plus that from the sea) is broken down by high-shore amphipods and eventually supplies detritus-based food webs in nearshore ecosystems. Insects are important to fishes such as juvenile salmon that forage on the shore at high tide as they migrate out of the Sound; complex marine habitats such as those provided by eelgrass beds are also critical for

these species (reviewed in Fresh, 2006). Other animals (for example, other fishes) from nearshore waters probably use the beach at high tide, although these linkages have had little documentation. Nearshore waters are critical to the beach, in turn, by bringing food for the abundant suspension feeders, as well as larvae, spores, and seeds of shoreline organisms, nearly all of which have dispersive propagules. Finally, humans use the shore of Puget Sound extensively, for both extractive (harvesting of clams and other shellfish, as well as algae) and non-extractive (education, birdwatching, walking) activities (Leschine and Petersen, 2007).

Armoring on Puget Sound Beaches

As mentioned above and elsewhere in this volume, a large proportion of the shoreline of Puget Sound, approximately 25–30 percent, is armored (Strategic Needs Assessment Report, 2009). The proportion is much higher in the south-central Sound, around 63 percent, than further north. In some cases armoring is installed primarily as a landscaping feature; this is especially true on muddy shores, which (as low-energy environments) are vulnerable to much less erosion than more open beaches in Puget Sound. In other environments, especially the high shore above mixed-fine, sand, and cobble beaches, armoring is used to protect property from erosion or perceived risk of erosion. A variety of studies (mentioned above, and see review by Coyle and Dethier, 2010) have demonstrated ecological impacts of armoring on high-shore processes, especially when the armoring is emplaced below Ordinary High Water such that it covers the supratidal zone and interrupts terrestrial-marine linkages. In other parts of the world, armoring has been demonstrated to cause local beaches to become steeper and coarser; if that occurs in Puget Sound, this change in substrate type would be expected to have an impact on the local flora and fauna. However, this effect has not been demonstrated locally, and we do not know how far across the shore (for example, into the low intertidal) or along the shore (that is, down-drift) such impacts might occur. Substantial research that spans various spatial and temporal scales is needed to understand these impacts.

References Cited

- Allee, R.J., Dethier, M., Brown, D., Deegan, L., Ford, R.G., Hourigan, T.F., Maragos, J., Schoch, C., Sealey, K., Twilley, R., Weinstein, M., and Yoklavich, M., 2000, Marine and estuarine ecosystem and habitat classification: National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-43, 43 p.
- Auffrey, L.M., Robinson, S.M.C., and Barbeau, M.A., 2004, Effect of green macroalgal mats on burial depth of soft-shelled clams *Mya arenaria*: Marine Ecology Progress Series: v. 278, p. 193–203.
- Bailey, A., Berry, H., Bookheim, B., and Stevens, D., 1998, Probability-based estimation of nearshore habitat characteristics, *in* Puget Sound Research Conference, Seattle, Wash., 1998, Proceedings: Seattle, Wash., Puget Sound Partnership. Available at: http://www.dnr.wa.gov/ResearchScience/Topics/AquaticHabitats/Pages/aqr_nrsh_publications.aspx.
- Bolam, S.G., Fernandes, T.F., Read, P., and Raffaelli, D., 2000, Effects of macroalgal mats on intertidal sandflats—An experimental study: *Journal of Experimental Marine Biology and Ecology*, v. 249, p. 123–137.
- Brennan, J.S., 2007, Marine riparian vegetation communities of Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2007-02.
- Buchanan, J.B., 2006, Nearshore birds in Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2006-05. (Available at <http://www.pugetsoundnearshore.org>.)
- 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, p. 245–266.
- Dethier, M.N., 1990, A Marine and Estuarine Habitat Classification System for Washington State: Olympia, Wash., Natural Heritage Program, Washington Department of Natural Resources, 60 p.
- Dethier, M.N., 2006, Native shellfish in nearshore ecosystems of Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2006-04. (Available at <http://www.pugetsoundnearshore.org>.)
- Dethier, M.N., and Berry, H.D., 2009, Puget Sound intertidal biotic community monitoring—2008 monitoring report: Olympia, Wash., Washington State Department of Natural Resources.
- Dethier, M.N., Ruesink, J., Berry, H., Sprenger, A.G., and Reeves, B., 2010, Restricted ranges in physical factors may constitute subtle stressors for estuarine biota: *Marine Environmental Research*, v. 69, p. 240–247.

- Dethier, M.N., and Schoch, G.C., 2005, The consequences of scale—Assessing the distribution of benthic populations in a complex estuarine fjord: *Estuarine, Coastal and Shelf Science*, v. 62, p. 253–270.
- Dugan, J.E., Hubbard, D.M., Rodil, I.F., Revell, D.L., and Schroeter, S., 2008, Ecological effects of coastal armoring on sandy beaches: *Marine Ecology*, v. 29, p. 160–170.
- Dumbauld, B.R., and Wyllie-Echeverria, S., 2003, The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA: *Aquatic Botany*, v. 77, p. 27–42.
- Eissinger, A., 2007, Great Blue Herons in Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2007-06 (Available at <http://www.pugetsoundnearshore.org>.)
- Fresh, K.L., 2006, Juvenile Pacific salmon in Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2006-06. (Available at <http://www.pugetsoundnearshore.org>.)
- Glude, J.B., 1978, The clam genera *Mercenaria*, *Saxidomus*, *Protothaca*, *Tapes*, *Mya*, *Panope*, and *Spisula*—A literature review and analysis of the use of thermal effluent in the culture of clams: *Aquaculture Consultant Report*, 74 p.
- Kozloff, E.N., 1993, *Seashore life of the northern Pacific coast—An illustrated guide to northern California, Oregon, Washington, and British Columbia*: Seattle, Wash., University of Washington Press.
- Leschine, T.M., and Petersen, A.W., 2007, Valuing Puget Sound’s valued ecosystem components: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2007-07. (Available at <http://www.pugetsoundnearshore.org>.)
- Madden, C.J., Goodin, K., Allee, R.J., Cicchetti, G., Moses, C., Finkbeiner, M., and Bamford, D., 2009, Coastal and marine ecological classification standard (ver. 3): National Oceanic and Atmospheric Association and NatureServe, 126 p. (Available at <http://www.csc.noaa.gov/benthic/cmecs/>.)
- McKernan, D.L., Tartar, V., and Tollefson, R., 1949, An investigation of the decline of the native oyster industry of the State of Washington, with special reference to the effects of sulphite pulp-mill waste on the Olympia oyster (*Ostrea lurida*): Gig Harbor, Wash., Washington State Department of Fisheries, Bulletin No. 49-A:117–165.
- Mumford, T.M., 2007, Kelp and eelgrass in Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2007-05. (Available at <http://www.pugetsoundnearshore.org>.)
- Penttila, D., 2007, Marine forage fishes in Puget Sound: Seattle, Wash., U.S. Army Corps of Engineers, Puget Sound Nearshore Partnership Report No. 2007-03. (Available at <http://www.pugetsoundnearshore.org>.)
- Pister, B., 2009, Urban marine ecology in southern California—The ability of riprap structures to serve as rocky intertidal habitat: *Marine Biology*, v. 156, p. 861–873.
- Rice, C.A., 2010, Biological effects of shoreline armoring in Puget Sound—Past studies and future directions for science, 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, p. 155–160.
- Schink, T.D., McGraw, D.A., and Chew, K.K., 1983, Pacific coast clam fisheries: Washington Sea Grant Technical Report WSG83-1, 72 p.
- Schoch, G.C., and Dethier, M.N., 1997, Analysis of shoreline classification and bio-physical data for Carr Inlet (FY97-078, Task 1 and Task 2): Report to the Washington State Department of Natural Resources.
- Shipman, H., 2010, The geomorphic setting of Puget Sound—Implications for shoreline erosion and the impacts of erosion control structures, 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, p. 19–34.
- Strategic Needs Assessment Report (SNAR), 2009, Strategic Needs Assessment Report (Draft): Prepared in support of the Puget Sound Nearshore Partnership and PSNERP Strategic Needs Assessment Team, Anchor QEA, Coastal Geologic Services Inc.
- Thom, R.M., 1984, Composition, habitats, seasonal changes and productivity of macroalgae in Grays Harbor Estuary, Washington: *Estuaries*, v. 7, p. 51–60.
- Thom, R.M., 1989, Plant standing stock and productivity on tidal flats in Padilla Bay, Washington—A temperate North Pacific estuarine embayment: University of Washington, Fisheries Research Institute Padilla Bay National Estuarine Research Reserve Reprint Series No. 13, Report to NOAA/OCRM/MEMD (FRI-UW-8909), 37 p.
- Thom, R.M., and Albright, R.G., 1990, Dynamics of benthic vegetation standing-stock, irradiance, and water properties in central Puget Sound: *Marine Biology*, v. 104, no. 1, p. 129–141.

Thom, R.M., Parkwell, T.L., Niyogi, D.K., and Shreffler, D.K., 1994. Effects of graveling on the primary productivity, respiration and nutrient flux of two estuarine tidal flats: *Marine Biology*, v. 118, p. 329–341.

Toft, J.D., Cordell, J.R., Heerhartz, S.M., Armbrust, E.A., and Simenstad, C.A., 2010, Fish and invertebrate response to shoreline armoring and restoration in Puget Sound, *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, p. 161-170.

Washington State Department of Natural Resources, 2010, Summary of key findings—ShoreZone inventory: Washington State Department of Natural Resources website, accessed November 4, 2010, at http://www.dnr.wa.gov/Publications/aqr_nrsh_shrzne_sum_find.pdf.

Suggested Citation

Dethier, M.N., 2010, Overview of the ecology of Puget Sound beaches, *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, p. 35-42.

This page intentionally left blank.