



SECTION 2
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Larrabee State Park, Bellingham, Washington
Photo: Nick Pinkham

SECTION 2

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Photo: Taylor Bayly

SALISH SEA BIOPHYSICAL PROCESSES

The Salish Sea is a complex waterbody defined by freshwater and marine water that mix in two primary basins and numerous subbasins carved by glacial history. While we think of this waterbody as the estuary that is the Salish Sea, these basins are strongly influenced by their surrounding watersheds. The watersheds and the subbasins they flow into have unique physical characteristics that shape the complex geography, oceanography, and biota within them and contribute to differences in response to urbanization and climate change. Many of those characteristics and ecological interdependencies that define the Salish Sea and drive its biophysical processes are described in this subsection.

Geology and Hydrology

Today, the Salish Sea is framed by more than 9,400 km (5,850 mi) of shoreline, including mainland and island shores (Flower 2020; see Figure 1.1). The landscape that surrounds and underlies the Salish Sea has been influenced on geologic timescales by the tectonics associated with the Pacific and North America plate boundary along the outer coast of Oregon, Washington, and British Columbia where the Cascadia Subduction Zone accommodates

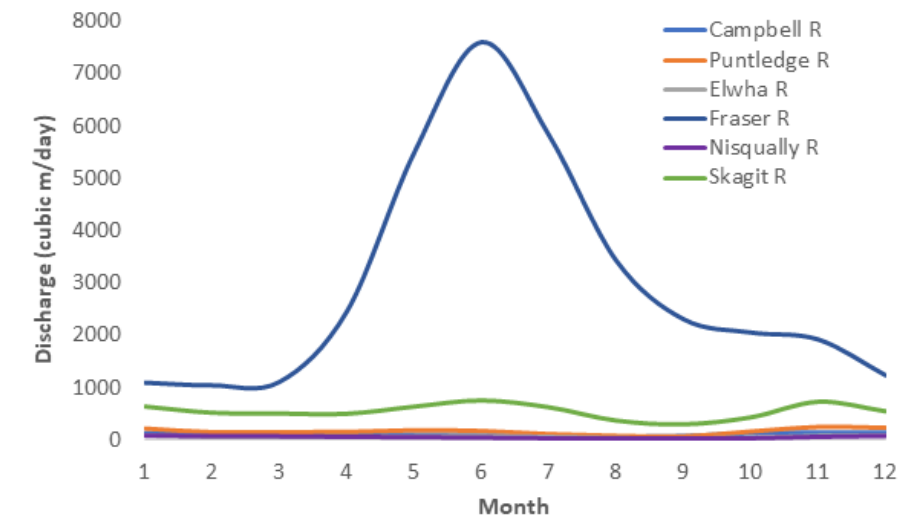
convergent plate motions. Associated with this, folding, uplift, and faulting contributed to the Georgia Depression and Puget Lowlands regions since at least the Cretaceous period (~150 million years ago; Dash et al. 2007). During the Pleistocene, multiple glaciations carved hills and valleys and created the surface geology that characterizes the Salish Sea.

About 14,000 years ago, slow moving glaciers receded north across the existing Georgia Depression, forming the basins of Puget Sound, Strait of Georgia, and the Strait of Juan de Fuca. Meltwater flowing beneath the glaciers is believed to have scoured the major troughs that define the Salish Sea today (Booth 1994), and most of the sediment exposed on the edges of river valleys and along the coastal bluffs is glacially derived. The current geophysical configuration of the Salish Sea is a function of the complex shape of the waterbody and the geology of the coastline, combined with the glacial deposits that have been redistributed by waves, tides, and rivers over time (Shipman 2008). The resulting landscape features along the shoreline include coastal bluffs, estuaries, rocky shores, barrier beaches, and river deltas. The watersheds surrounding the Salish Sea are also complex and are a defining aspect of



Left: Figure 2.1. The Fraser River plume, southern Strait of Georgia, Admiralty Inlet, Whidbey Basin, and the San Juan and Gulf Islands, as seen by the European Space Agency's Copernicus satellite. Source: European Space Agency 2021

Right: Figure 2.2. Average discharge from a subset of rivers flowing into the Salish Sea. Mean values aggregated by month and averaged from 1999-2016 show how much greater the freshwater input is from the Fraser River compared to other rivers. Data from Washington Department of Ecology.



70% of the freshwater in the Strait of Georgia (Johannessen et al. 2003). Though much smaller than the Columbia River in both watershed size and annual discharge—the Columbia averages 7,500 m³/s (265,000 ft³/s), while the Fraser averages 3,475 m³/s (122,700 ft³/s)—the Fraser is a dominant feature within the Salish Sea, contributing freshwater and driving circulation throughout the system (Figure 2.2). Of the 240,000 km² (92,660 mi²) in the watershed (Déry et al. 2012), only the Lower Fraser River basin is within the Salish Sea bioregion. Much of the Fraser River watershed is east of the bioregion boundary, but salmon migrating upstream into the British Columbia interior and the massive spring freshet (averaging about 7,000 m³/s/d; Curry & Zwiers 2018) flowing to the sea are a reminder of the connectivity between the upper basins and the Salish Sea (Déry et al. 2012).

The Fraser River may be the dominant source of freshwater in the Salish Sea as a whole, but

other freshwater sources are important locally for bringing sediment and freshwater to their deltas and estuarine wetlands (Figure 2.3). Other major freshwater inputs include the Campbell, Puntledge, Big Qualicum, Englishman, Cowichan, Powell, Squamish, Cedar, Duwamish/Green, Elwha, Nisqually, Nooksack, Puyallup, Skagit, Skokomish, Snohomish, and Stillaguamish Rivers. Seasonal influxes of freshwater vary considerably.

For all river systems, lower volume base flows occur in late summer. Peak flows occur in mid-winter in rain-dominated systems and in early summer in snow-dominated systems, where melting winter snow generates a spring freshet (e.g., Fraser, Nooksack, and Skagit Rivers among others; Morrison et al. 2012). The variation in freshwater inflow across the year has implications for estuarine circulation, but also for changing sediment delivery, salinities, and temperatures in lower portions of rivers and the **nearshore**, impacting organisms living there (Figure 2.4).

the ecoregion, from the crests of the Cascade, Olympic, and Coast Mountains and Vancouver Island Ranges to the saltwater shorelines of the Salish Sea. The 17,803 km² (6,874 mi²; Flower 2020) of the estuarine waters of the Salish Sea are freshened by several major rivers and the additional freshwater runoff from approximately 45 watersheds. In total, these watersheds comprise almost 320,000 km² (124,000 mi²) of land area (Flower 2020). Streams and rivers within the watersheds serve as ecological corridors that

transport freshwater, sediment, organic matter, organisms, and nutrients downstream where they influence the estuarine ecosystem; in turn, species like Pacific salmon, smelt, and seabirds deliver ocean-derived nutrients to the uplands.

The Fraser River is the dominant source of freshwater and sedimentary particles to the Salish Sea (Figure 2.1). It contributes approximately 50% of the freshwater entering the Salish Sea system (Khangaonkar et al. 2018) and more than

Nearshore

The area that extends from the head of tide (the uppermost reach of tidal influence) in water and the upper edge of coastal bluffs on land seaward to the offshore limit of the photic zone is referred to as the nearshore.

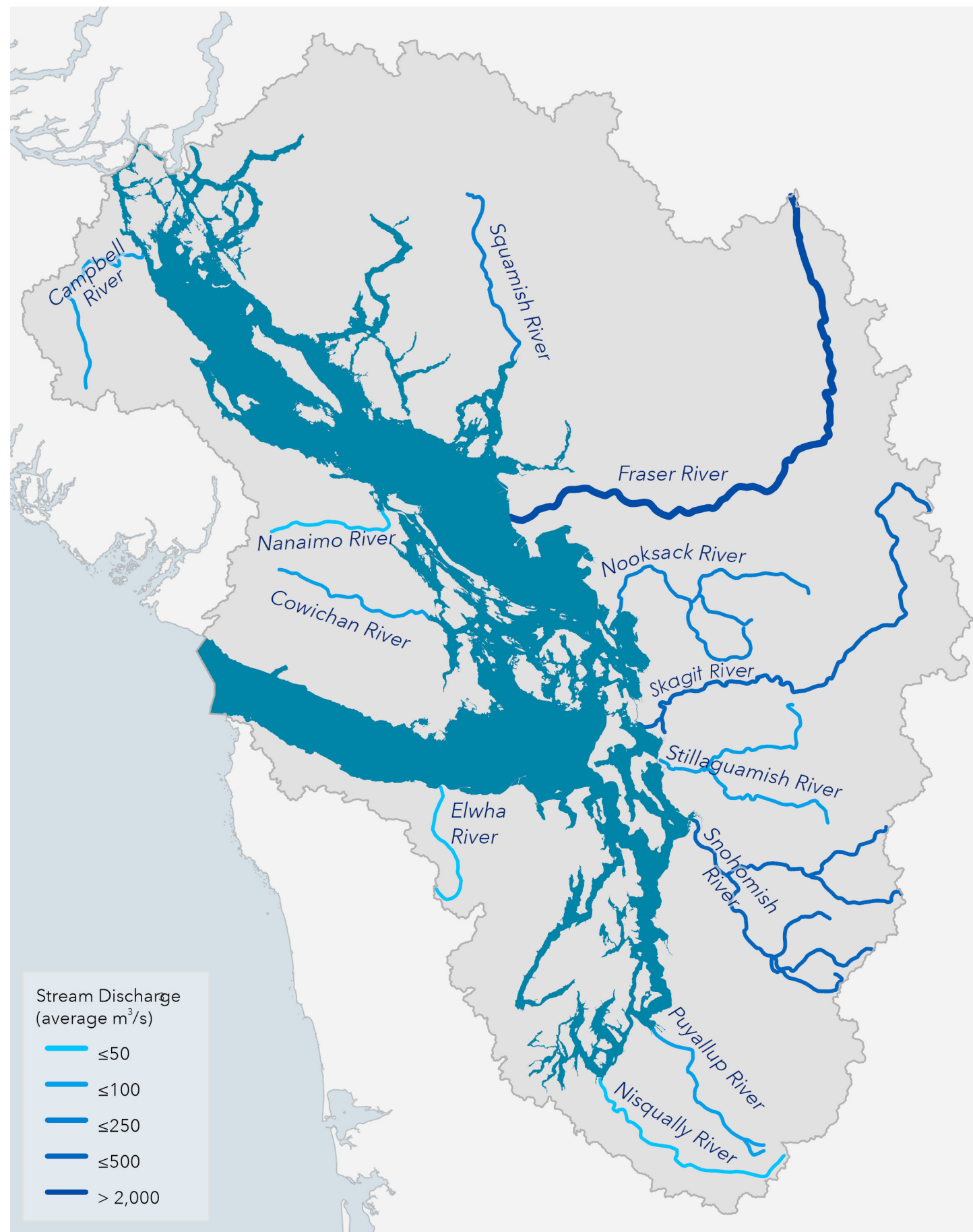


Figure 2.3. Major rivers of the Salish Sea and average stream discharge (cubic meters per second). Data are based on annual averages from 1981 to 2010. Map by Aquila Flower, 2021. CC BY-NC-SA 4.0 License. Data from Environment Canada, US Geological Survey, and the Salish Sea Atlas.

Terrestrial Ecology

The terrestrial landscapes within the watersheds that drain into the Salish Sea are largely dominated by highly productive coniferous forests, where many of the conifer species reach their maximum growth potential for height and diameter (Franklin & Dryness 1998). The lowland forests in the Salish Sea were once mostly dominated by dense coniferous forests, commonly made up of western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), and Douglas fir (*Pseudotsuga menziesii*) interspersed with hardwoods, such as bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*). This dominant flora remains in some areas. On drier sites, Garry oak (*Quercus garryana*), Pacific dogwood (*Cornus nuttallii*), and arbutus (*Arbutus menziesii*, also called madrone) are common. Open areas resulting from soil conditions and human practices occurred throughout the forests (Charnley et al. 2008). Early Indigenous peoples used a variety of practices to maintain forests for production of food and products, including burning, pruning, tilling, and transplanting (Turner et al. 2013). Today, many of the lowland forests have been converted to urban or agricultural land, although stands of forest remain in some areas.

Vegetation within riparian corridors along rivers and streams plays an especially important role in regulating freshwater input and quality to the Salish Sea (Naiman et al. 2000). For example, during high stream flows, riparian vegetation slows and dissipates floodwaters, which helps reduce erosion and sediment load that continues downstream. In many other ways, riparian zones are important in maintaining watershed hydrology, stream flows, water quality, stream nutrients, and habitat characteristics needed to maintain native aquatic species (Naiman et al. 1992).

Vegetation along shorelines, river deltas, sloughs, and tidal floodplains is important in regulating freshwater and nutrient exchange, as well as temperature and organic matter flux, serving as an important ecotone between terrestrial and estuarine ecosystems. Shoreline vegetation, also known as marine riparian vegetation (Brennan 2007), includes the common conifers of upland forests, as well as Sitka spruce (*Picea sitchensis*), shore pine (*Pinus contorta*), and hardwoods like red alder, bigleaf maple, and madrone (arbutus), along with numerous shrubs, such as oceanspray (*Holodiscus discolor*) and salal (*Gaultheria shallon*). Local variations in soils, temperature, exposure to sun and wind, precipitation, topography, soil stability, tidal inundation, and microclimate cause small-scale variations in vegetation community types throughout the watersheds but along the estuarine shorelines, salt exposure is also a defining factor (Levings & Jamieson 2001). Buffered shorelines along both fresh and marine waters protect ecological processes and critical habitats for organisms in this important region of exchange.

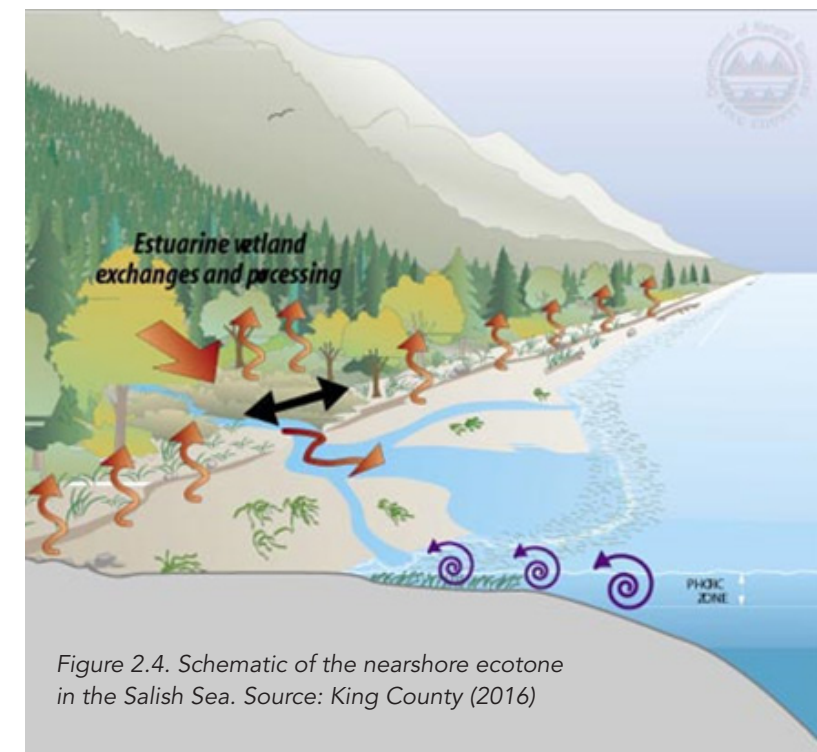


Figure 2.4. Schematic of the nearshore ecotone in the Salish Sea. Source: King County (2016)

Primary Basins and Subbasins

The combination of freshwater input from the watersheds and Pacific Ocean-derived marine waters gives the Salish Sea its unique oceanography and ecology. The main connection of the Salish Sea to the Pacific Ocean is through the Strait of Juan de Fuca, with a smaller connection at the north end of the Strait of Georgia through Johnstone Strait. The two primary basins are the Strait of Georgia and Puget Sound, but the Salish Sea is further divided into subbasins by a series of sills (Figure 2.5). These submarine ridges are important bathymetric features and geospatial reference points because they influence the circulation of water and bathymetrically define subbasins within the Salish Sea.

The Strait of Juan de Fuca forms the channel between Vancouver Island and Washington State, with the international boundary running down the middle of the Strait. Its depth decreases eastward, from about 250 m (820 ft) at its western end where it meets the Pacific Ocean to 55 m (180 ft) in the sill region at its eastern extent (Thomson 1981). At its eastern end, the Strait of Juan de Fuca bifurcates to form the channels of the San Juan/Gulf Islands archipelago, including Haro and Rosario Straits connecting the Strait of Juan de Fuca to the Strait of Georgia to the north, with Admiralty Inlet leading southward to Puget Sound.

The Strait of Georgia is large (surface area of about 9,000 km² or 3,500 mi²) and deep, with an average depth of 155 m (509 ft) (Thomson 1981). The Strait has two deep basins: a south-central basin with maximum depths of about 445 m (1,460 ft) and a northern basin with maximum depths of about 760 m (2,493 ft). Texada Island, the largest of the Gulf Islands, separates the

south-central and northern parts of the Strait, with a 170 m (558 ft) sill on the southwestern side. Malaspina Strait, an area of high current, runs along the east side of the island bordering the British Columbia mainland.

The northern exit of the Strait of Georgia consists of narrow and relatively shallow passages through numerous islands in the Desolation Sound region, eventually passing through Johnstone Strait, a constricted passage with strong current (Beamish & McFarlane 2014). The northern passage comprises only 7% of the cross-sectional area of all exits from the Strait of Georgia but has been estimated to carry about 17% of the outflow (Pawlowicz et al. 2007). These waters eventually empty into Queen Charlotte Sound on the central coast of British Columbia. The Strait of Georgia also has several large fjords on the mainland side of the Strait, with a variety of striking oceanographic and biological characteristics (e.g., Sechelt Inlet and its Skookumchuck Narrows).

Puget Sound has a surface area of about 2,600 km² (1,004 mi²) and is divided into several subbasins. These subbasins are bathymetrically defined by the presence of sills that constrict the flow of water from one subdivision of the Puget Sound Basin to the next (Cannon 1983). The subbasins of Puget Sound include Admiralty Inlet, Main Basin (sometimes called Central Basin or Central Puget Sound), Whidbey Basin, South Puget Sound, and Hood Canal (Williams et al. 2001). Main Basin is the largest and has the greatest volume of water of any subbasin in Puget Sound, with depths ranging from 65 m (213 ft) at Admiralty Inlet to 270 m (886 ft) deep farther south. Whidbey Basin, which sits to the east of Whidbey Island, is unique in that there is

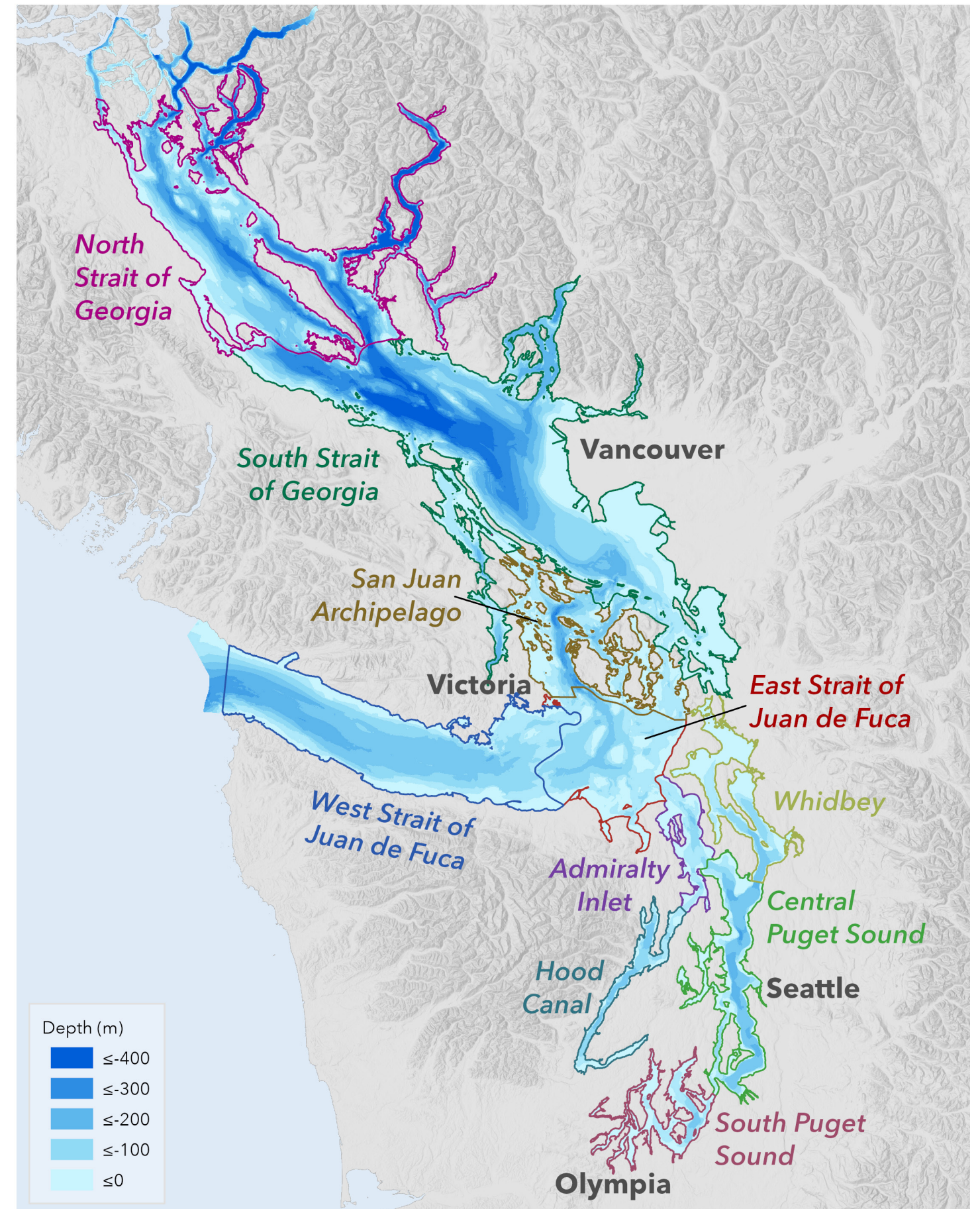


Figure 2.5. Subbasins and bathymetry of the Salish Sea. Basins are delineated based on water depth and circulation. Shallower areas associated with underwater sills separate many of the basins, creating distinct oceanography. Map by Aquila Flower, 2021. CC BY-NC-SA 4.0 License. Data from NOAA, BC Freshwater Atlas, US Geological Survey, and the Salish Sea Atlas.

no sill across the entrance; therefore, it is defined more by geography than bathymetry. It is a much shallower basin, with a much higher percentage of tidelands than any of the other basins. In addition, Whidbey Basin has three major freshwater sources in the Stillaguamish, Snohomish, and Skagit Rivers, the latter of which delivers about half of the freshwater flow to Puget Sound. South Puget Sound is defined by a sill at the Tacoma Narrows. The sill is 45 m (148 ft) deep but the maximum depth of the South Puget Sound basin (167 m or 548 ft) occurs just on its south side. The mean depth in South Puget Sound is only 32 m (105 ft) and, like Whidbey Basin, the relatively shallow depth yields large areas of tidelands. South Puget Sound is also defined by numerous islands and complex shorelines around many inlets.

The distinct geological and oceanographic characteristics of the subbasins means circulation, residence time, water chemistry, physical properties and biota are variable on small spatial scales across the ecosystem. Most previous studies have treated Puget Sound and the Strait of Georgia basins as separate entities given regional differences in oceanography and the international border and distinct research enterprises on either side. However, increasing numbers of researchers are studying the oceanography of the Salish Sea in its entirety (Sutherland et al. 2011; Khangaonkar et al. 2018, 2019; Barth et al. 2019; MacCready et al. 2020). The resulting models and research approaches are becoming more integrated across the border and will further unify understanding of biological and physical oceanography within the Salish Sea.

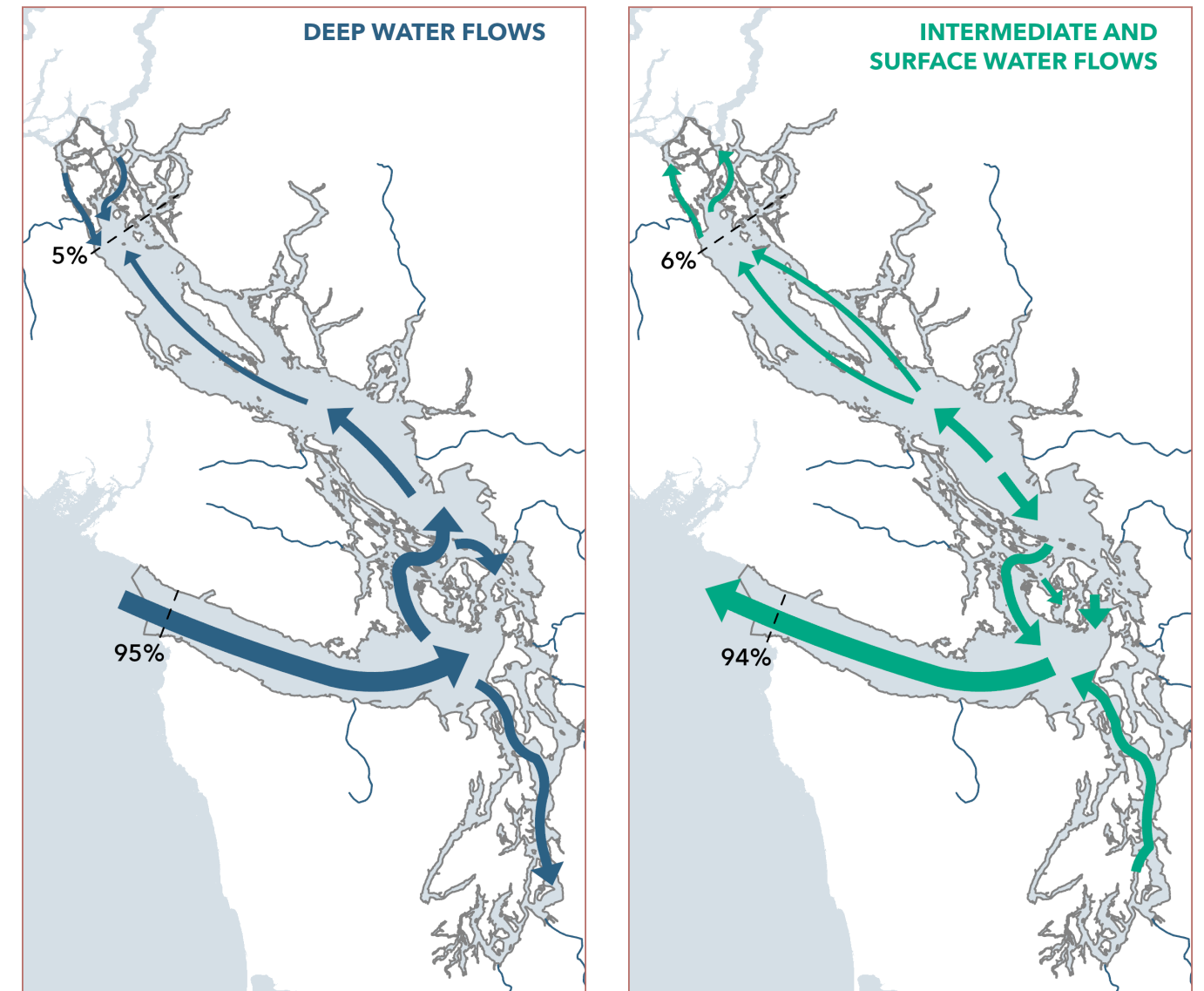


Figure 2.6. Direction and relative magnitude (line width) of net water flow in the Salish Sea. Deep water flows represent primarily marine waters entering the Salish Sea from the Pacific Ocean. Intermediate depth and surface flows represent a mix of marine waters and freshwater from rivers in the Salish Sea. Actual circulation patterns are highly complex and seasonally variable, this diagram shows a simplified model of net exchanges. Labels indicate percent of the total water exchange that moves in and out of the Salish Sea through the Strait of Juan de Fuca in the south and through the northern boundary of the Strait of Georgia. Map by Aquila Flower, 2021. CC BY-NC-SA 4.0 License. Data from the Salish Sea Atlas.

Circulation and Mixing

The circulation patterns in the sill-basin system of the Salish Sea are estuary-like. The large amount of freshwater entering at the surface through rivers in Puget Sound and the Strait of Georgia—especially the Fraser River—drives a multi-layer flow, with fresher water flowing west toward the Pacific Ocean and the denser Pacific Ocean waters flowing east into the Salish Sea at depth through the Strait of Juan de Fuca (Geyer & Cannon 1982; Figure 2.6). This is known as estuarine exchange flow (Figure 2.7). The deep saline inflow from the Pacific Ocean travels through the Strait of Juan de Fuca and over a series of shallow sills where it mixes with the overlying fresh (and less dense) surface waters travelling seaward (Soontiens & Allan 2017). Mixing is modulated by tidal currents creating turbulent mixing in a mid-layer and results from the spring and neap tidal cycle on short time scales (Figure 2.7, middle panel), with higher mixing rates during the spring tides when tidal currents are stronger (Soontiens & Allan 2017). Wind also drives mixing and water movement and patterns change seasonally. Seasonal cycles in freshwater outflow mediate mixing and circulation on annual timescales. Water exiting the Salish Sea through Johnstone Strait and the Strait of Juan de Fuca is relatively salty (30–32 ppt, seasonally variable) due to tides and currents and the turbulence induced at the shallower sills throughout the Salish Sea system (Martin & MacCready 2011). It is not uncommon for the movement of water at the immediate surface to be counter to that in the mid-layer and/or at depth (Stevens et al. 2021; S. Allen, University of British Columbia, personal communication), creating complex circulation patterns.

The low-density fresh or brackish waters can sit atop deeper layers of saltwater and be relatively resistant to vertical mixing. When there is a strong density difference between the layers (known as a pycnocline), stratification between layers may occur. Stratification is more common in the basins of the Strait of Georgia and Puget Sound than in the Strait of Juan de Fuca, but mixing and stratification of water types is patchy in time and space throughout the Salish Sea (Sutherland et al. 2011).

The transport of ocean water into and freshwater out of the Salish Sea decreases the residence time of waters within this inland body of water. In Puget Sound, it is estimated that the freshwater filling time based on river flow alone is approximately 5 years; however, after accounting for the exchange flow generated by the surface movement of freshwater out of the region and deep ocean water into the region, the estimated residence time is dramatically reduced to 90–180 days (Babson et al. 2006). The steep reduction in residence time is an expression of the relative size of the exchange flow, which is roughly 20 times greater than the sum of all the rivers (Sutherland et al. 2011). In the Strait of Georgia, the residence time is highly variable by season, with longer surface residence times in the winter, when Fraser River discharge is lower (Pawlowicz et al. 2019). Circulation and an understanding of the processes that control the exchange and mixing of oceanic and freshwater are critical and play a central role as environmental issues, such as hypoxia (i.e., low concentrations of dissolved oxygen), pollution, ocean acidification, and climate change continue to be of concern in the Salish Sea (Sutherland et al. 2011; Khangaonkar et al. 2018).

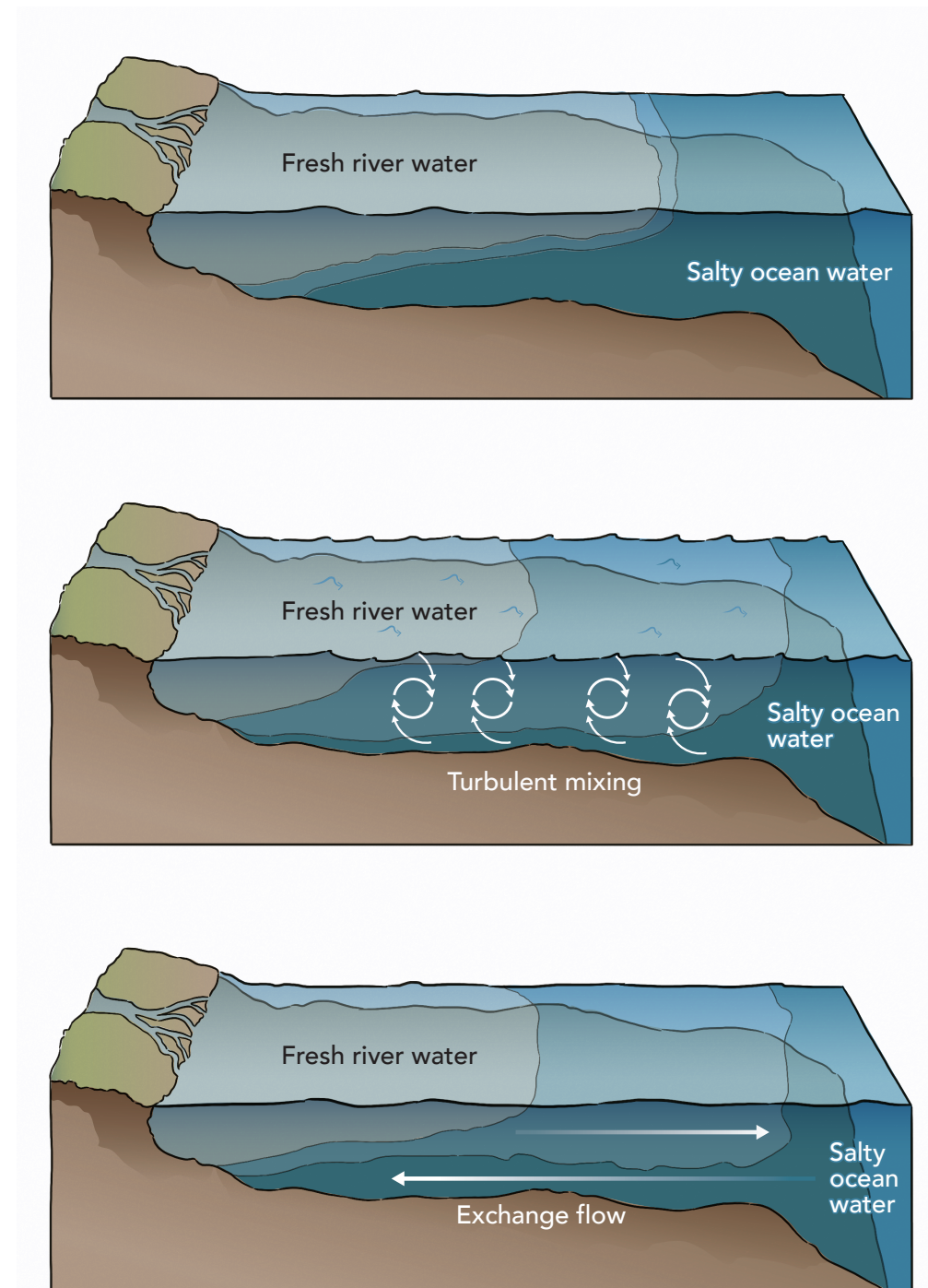


Figure 2.7. Schematic diagram of exchange flow in the Salish Sea. Freshwater from the Fraser River flows at the surface out into the Strait of Georgia and Strait of Juan de Fuca while salt water from the Pacific Ocean enters the Strait of Juan de Fuca at depth (top panel). Turbulent mixing caused by tides, currents, and estuarine circulation mixes the water masses (middle panel). Mixed salinity water exits back to the Pacific Ocean near the surface creating the exchange flow (bottom panel), which drives estuarine circulation in the Salish Sea. Illustration by Emily Eng for the Salish Sea Institute, adapted from P. MacCready, University of Washington.

Productivity and Marine Ecology

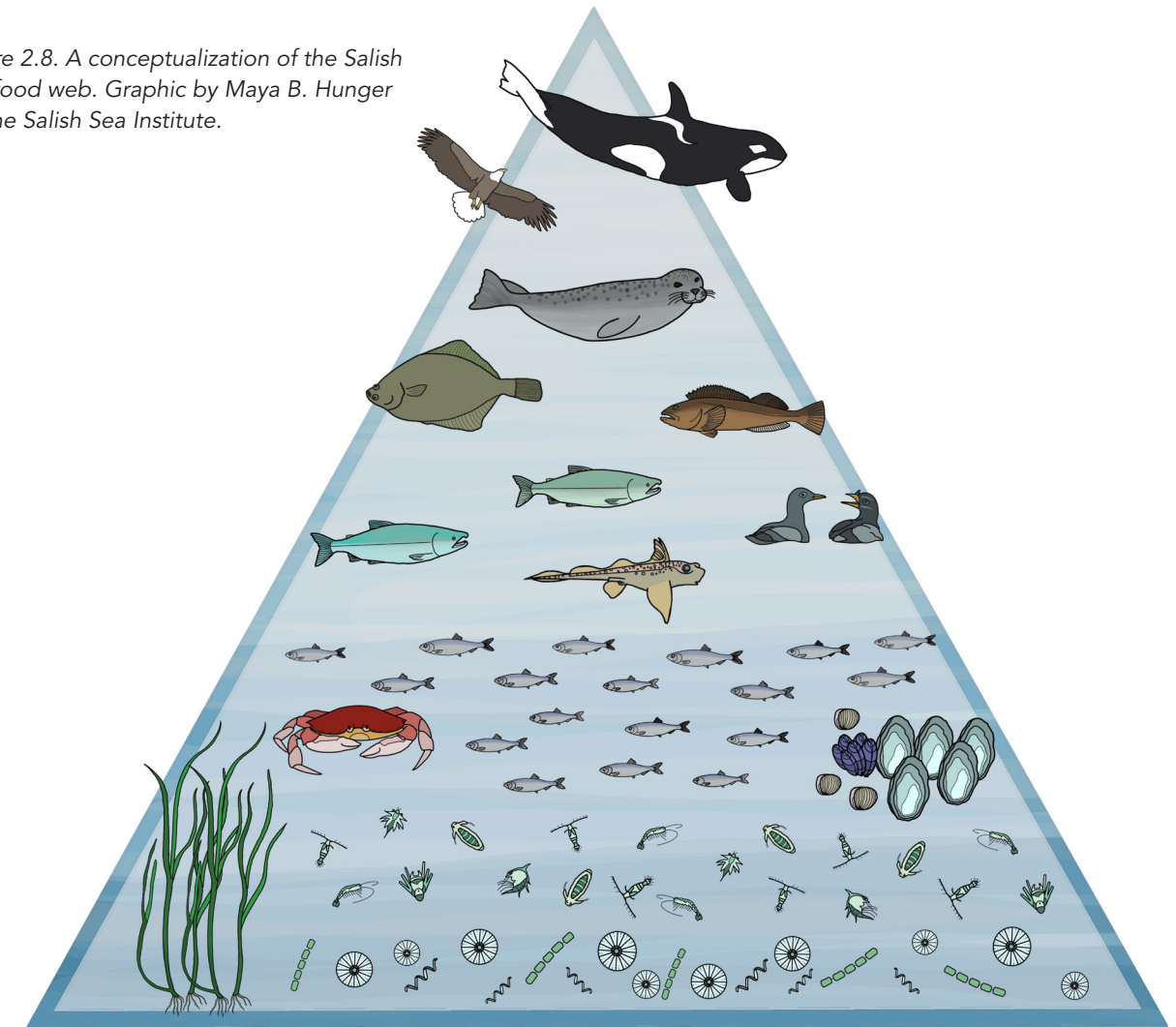
The geology, bathymetry, and physical features of the Salish Sea can strengthen or weaken biological productivity by affecting nutrient delivery via the mixing process. However, biological productivity within the system is largely driven by marine sources (Conway-Cranos et al. 2015). This marine-driven productivity is an important feature of the Salish Sea estuary. Vertical mixing benefits primary production in that it brings ocean-derived nutrients up from deeper water layers towards the surface, where light is abundant but nutrients are less plentiful. For photosynthesis to occur, a balance between mixing and stratification is necessary because mixing can drive plankton deeper and out of the photic zone (the upper-most layer where light is available for photosynthesis). As precipitation and snowmelt peaks in the spring, an influx of freshwater to the surface layers combines with lengthening days and greater solar input and phytoplankton growth surges. During this time, stratification is maintained by relatively calm weather, creating a strong pycnocline and ample sunlight to facilitate photosynthesis.

The high productivity of biota in the Salish Sea is driven by abundant nutrients, specifically nitrogen, entering the Sea from Pacific Ocean water (Mackas & Harrison 1997; Davis et al. 2014). This nitrogen-rich water mixes with surface waters as it circulates from the entry in the Strait of Juan de Fuca throughout the Strait of Georgia and Puget Sound basins (see Vignette 1, The Salish Sea Estuary System). A lesser amount of nutrients, some of which,

like silica, are critically important to the base of the food web, comes from freshwater inputs. Weathering from the mountain ranges and rocks brings essential macronutrients like phosphate and silica into the Salish Sea. These nutrients, delivered to the estuary by both ocean water and freshwater, are the raw material with which microplankton and phytoplankton build their cell walls, forming the base of the food web.

Phytoplankton form the base of marine food webs as the dominant photosynthetic producers. They influence water chemistry and nutrient dynamics in space and time, and their distributions are driven by the availability of light and nutrients. Major groups of phytoplankton in Salish Sea waters include diatoms, dinoflagellates, and nanoflagellates. The phytoplankton community in the Salish Sea is dominated by centric, chain-forming diatoms (Esenkulova & Pearsall 2016; Nemcek et al. 2020). Diatoms are a major food source for a wide variety of zooplankton, including larger species that are important prey for fish. In contrast, dinoflagellates and nanoflagellates generally flourish under lower nutrient conditions, as in winter in the Salish Sea. There is a seasonal progression from diatom-dominated communities in the spring when light and nutrients are abundant to more diverse communities of smaller, motile (flagellated) types of phytoplankton in the summer as grazing occurs and stratification makes nutrients less available (see Vignette 2, Lower Trophic Levels in the Salish Sea).

Figure 2.8. A conceptualization of the Salish Sea food web. Graphic by Maya B. Hunger for the Salish Sea Institute.



The Salish Sea zooplankton community is composed chiefly of copepods, which graze on diatoms, especially at the surface where phytoplankton prey are readily available. Recent studies from the Strait of Georgia found that copepods (calanoid copepods in particular) dominated zooplankton by abundance, while larger crustaceans (euphausiids, amphipods, and decapods) and cnidarians (hydromedusae, ctenophores, and siphonophores) dominated by biomass (Young et al. 2017; Perry et al. 2021). Zooplankton distribution is determined by their physical dimensions and the characteristics of the environment. Mid- and deeper-water communities may consist of euphausiids, chaetognaths, and some deep-living copepods that are able

to overwinter at depth (Harrison et al. 1983). Distribution of zooplankton tends to be patchy in both space and time, as zooplankton respond to changing ocean currents and available prey. Horizontal patches of zooplankton may be important feeding sites for some fish species. The Salish Sea supports numerous other fauna critical in providing food for both humans and animal inhabitants. Macroinvertebrates, such as bivalve mollusks and crabs, are of subsistence, recreational, and commercial importance. Over 250 fish species swim in these waters, ranging from sharks to small gobies (Pietsch & Orr 2015), and include all five species of Pacific salmon, steelhead, and cutthroat trout. In addition, over 170 bird species rely on the habitats and

species found within the Salish Sea (Gaydos & Pearson 2011), with both resident and migratory species in high abundance (see Vignette 3, Birds of the Salish Sea).

Among all the fauna that rely on the marine-derived food web of the Salish Sea, the orca (*Orcinus orca*) is perhaps the most iconic species in the region. Although the orca may garner the greatest public attention, over 30 other marine mammals occur in the Salish Sea, including Dall's and harbor porpoise (*Phocoenoides dalli* and *Phocoena phocoena*, respectively), California sea lion (*Zalophus californianus*), and the harbor seal (*Phoca vitulina*). All of these species rely on an interconnected and highly productive food web.

The Salish Sea food web is like many other trophic webs that move energy and nutrients from one trophic level to another: from primary producers (e.g., phytoplankton) to higher trophic levels of secondary and tertiary consumers (e.g., zooplankton and fishes), and through decomposers (Figure 2.8). With each increasing trophic level, biomass declines. Trends in how the overall food web has changed over time are not well resolved, but there is some evidence that a trophic shift occurred over the last 30 years. Studies are ongoing to understand

the connections between primary production and upper trophic levels, like herring, Pacific salmon, and orcas. Recently, researchers in British Columbia began using trophic biomarkers (e.g., stable isotopes and fatty acids) to explore connections between phytoplankton and the availability of high-quality prey for juvenile Pacific salmon and Pacific herring in the Strait of Georgia (Costalago et al. 2020). They demonstrated that the plankton food web in the region is largely supported by both diatom and flagellate production, depending upon the season, and showed that spatial differences in energy transfer exist. The variation in community composition and energy transfer that the biomarkers showed provides evidence for differential productivity and growth within the Salish Sea.

While the Salish Sea is a single ecoregion, the series of sills, basins, and unique physical and chemical oceanography can all be strong mediating forces on biological production, particularly over short time scales and small spatial scales. Understanding variation in the Salish Sea is as important as understanding the characteristics that make this a contiguous estuarine ecosystem.

ESTUARINE BIOGENIC HABITATS

The pelagic (open water) marine environment makes up the largest proportion of habitat in the Salish Sea ecosystem. Across the **seascape**, there are also multiple biogenic structured habitats that provide refuge for organisms and myriad other ecosystem services. These estuarine biogenic habitats are connected with the pelagic realm via tides, currents, and circulation that drive fluxes of energy (biomass), sediments, and nutrients.

Highlighted in this subsection are four biogenic habitats: eelgrass beds, oyster reefs, kelp forests, and sponge reefs. While all four are sentinels of ecosystem change, two of these (eelgrass and kelp) receive much attention and are the subject of monitoring programs on both sides of the border. The other two (oysters and glass sponge reefs) are not as well understood and are thus featured here to highlight their historical and potential roles in maintaining resilience in the Salish Sea.

When species are considered together with the habitats they use, from the pelagic environment to biogenic habitats that are important for rearing and refuge, a more complete picture of ecological complexity and function becomes evident (Culhane et al. 2018). For example, native oysters were once an important natural occurrence within the Salish Sea and contributed structural habitat for other organisms. Restoration efforts highlight their habitat value, even though contemporarily, most people think of oysters in the context of commercial production (which is dominated by the introduced Pacific oyster, *Crassostrea gigas*). In another example, sponge reefs are being studied in Canada and are gaining attention for their high rates of carbon sequestration

and complex habitat. Protecting these kinds of habitats and the ecosystem services they provide is a promising way to mitigate the effects of global climate change.

Although not discussed in detail below, there are many additional and important benthic (bottom) habitats in the Salish Sea ecosystem, including intertidal mudflats, subtidal rocky reefs, mixed-substrate beaches, and rocky shorelines. Additionally, deltaic estuaries with complex channels and emergent, forested, and mixed-vegetation marshes along the freshwater to saltwater gradient were once common features at river mouths but have been much reduced due to development. Where they remain, they are important habitats for many invertebrate, fish, and bird species (Sutherland et al. 2013). Each of these biotopes provides habitat for a multitude of species, many of which move from across a mosaic of features, facilitating cross-habitat connectivity by moving nutrients and biomass throughout the ecosystem (Howe & Simenstad 2015; Chalifour et al. 2019).

Seascape

The term seascape (*sensu* Pittman et al. 2011) is used throughout this report to refer to the geographic and physical characteristics, including chemical properties, of the Salish Sea estuarine ecosystem. The complex spatial and geographic heterogeneity that exists on land (i.e., the landscape) does not end at the estuary's edge. Fundamentally landscape-like patterns associated with the geology and physical, chemical, and biological oceanography occur in estuarine and marine systems as well. These patterns drive variation in biodiversity of species, life history, and ecology within the seascape. Connectivity with the terrestrial and ocean ecosystems and their contributions to the Salish Sea estuarine seascape further defines this ecosystem.

Eelgrass

Eelgrass (*Zostera marina*) is a flowering plant that grows in shallow coastal waters throughout the northern hemisphere. Like most seagrasses, it prefers shallow soft substrate of sand and silt, where light is plentiful. Multiple factors determine eelgrass distribution, including substrate availability, water clarity, wave energy, light attenuation, water temperature, tidal amplitude, and desiccation stress (Hemminga & Duarte 2000; Thom et al. 2018). Eelgrass is patchy in distribution throughout the Salish Sea around the shorelines and islands (Wright et al. 2014), but is absent from the inlets of South Puget Sound (Christiaen et al. 2019). In the Salish Sea, eelgrass tends to occur as a linear band of fringing habitat along shorelines, from the intertidal zone to deepest edge of the photic zone, approximately 10 m (33 ft) in depth. The deepest beds are found where water clarity is greatest, such as in the Strait of Juan de Fuca and the San Juan Islands (Gaeckle et al. 2009). In addition to occurring as fringing habitat along beaches, eelgrass also is found in extensive beds at river deltas and in large flats, such as Padilla Bay, WA. Eelgrass is the most abundant of six seagrass species in the Salish Sea. The other five are: *Zostera japonica* (an introduced species), *Phyllospadix serrulatus*, *Phyllospadix scouleri*, *Phyllospadix torreyi*, and *Ruppia maritima*.

Eelgrass provides a multitude of ecosystem services. Through photosynthesis, eelgrass contributes to the global carbon cycle and carbon fixation that support local biota (Poppe & Rybczyk 2018; Prentice et al. 2020). It creates important biogenic habitat, and dense stands can help attenuate waves (Lacy & Wyllie-Echeverria 2011). Eelgrass also has been shown to contribute to waste treatment through the breakdown of contaminants, such as polycyclic aromatic hydrocarbons (PAHs) and

polychlorinated biphenyls (PCBs) (Huesemann et al. 2009). It offers numerous cultural services through bird watching, recreational fishing, and educational opportunities (Plummer et al. 2013), and eelgrass beds are valued harvesting grounds for Indigenous peoples (Cullis-Suzuki 2007; Wyllie-Echeverria & Ackerman 2003).

The biogenic habitat created by eelgrass makes up a small proportion of the Salish Sea seascape, yet it provides an outsized contribution to the nearshore ecosystem, is sensitive to change, and is relatively easy to monitor (Wright et al. 2014; Christiaen et al. 2019). Perhaps most notably, eelgrass supports a rich biota and provides important habitat for many fishes and invertebrates. For example, eelgrass provides structure for Dungeness crab (*Metacarcinus magister*) (Armstrong et al. 1988), offers spawning grounds for Pacific herring (*Clupea pallasii*) that use eelgrass blades as substrate for their eggs, and creates rearing opportunities for juvenile salmon (*Oncorhynchus spp.*) (Simenstad 1994; Kennedy et al. 2018). It also provides important feeding and foraging habitats for crustaceans, fishes, and waterbirds, such as black brant (*Branta bernicla*) (Wilson & Atkinson 1995).

Eelgrass supports multiple species of epiphytic algae that serve as a food source for numerous marine crustaceans, such as amphipods, isopods, and harpacticoid copepods, that are then consumed by higher trophic level species (Hayduk et al. 2019). Recent work using stable isotopes has shown evidence of epiphyte signatures in the tissues of fishes and invertebrates (Chittaro et al. 2020) in the Salish Sea, and eelgrass provides a substrate for these important algal primary producers. The importance of eelgrass epiphytes to the marine food web is well documented in other regions

(Valentine & Duffy 2006) including in the Pacific Northwest (Williams & Ruckelshaus 1993; Hayduk et al. 2019). Most eelgrass biomass enters the food web through detritus, as the blades senesce (deteriorate with age) and slough off seasonally with fall storms (McConnaughey & McRoy 1979; Howe et al. 2017). Some eelgrass detritus likely sinks into deeper water, but the fate and importance of this carbon source is unknown.

Eelgrass is one of the “Vital Signs” used by the Puget Sound Partnership (McManus et al. 2020) and the subject of numerous monitoring efforts in both Washington and British Columbia because of the extensive ecosystem services it provides and the fact that eelgrass responds rapidly to stressors (Thom et al. 2011; Yang et al. 2013; Wright et al. 2014). Monitoring in Puget Sound and the Strait of Georgia has largely been site specific, but larger-scale efforts are currently underway. The Washington State Department of Natural Resources maintains a considerable

monitoring effort and has systematically assessed eelgrass coverage for the last 20 years (Washington State Department of Natural Resources 2021). The total amount of eelgrass in Puget Sound has remained largely stable over this period, although localized losses and gains have occurred (Shelton et al. 2017). Recent research on eelgrass wasting disease highlights that while eelgrass losses are not considerable overall, threats to its health and persistence exist and may be exacerbated by warming seawater (see vignette on Eelgrass Wasting Disease in Section 4). In British Columbia, mapping and monitoring is undertaken by numerous groups associated with the Seagrass Conservation Working Group and its affiliates (Seagrass Conservation Working Group 2021). Although eelgrass losses in British Columbia are documented from shoreline development at specific sites (Nahirnick et al. 2020), identifying long-term trends in coverage is not possible without a transboundary monitoring program.



Deeper subtidal eelgrass shoots shimmering in False Bay, San Juan Island. Photo: Olivia Graham.

Kelp

Kelp forests are receiving increased attention as important biogenic habitats within the Salish Sea (Costa et al. 2020; Schroeder et al. 2020). Kelps are large brown seaweeds in the taxonomic order Laminariales. They are prominent members of the Salish Sea ecosystem and prefer shallow rocky bottoms where they can attach their holdfasts to suitable sized cobbles or bedrock and receive ample light for photosynthesis. More than 20 species of kelp are found in the Salish Sea (Mumford & Thomas 2007), among which are two primary species of floating canopy-forming kelp: the annual bull kelp (*Nereocystis luetkeana*) and the perennial giant kelp (*Macrocystis pyrifera*). *N. luetkeana* is the more common and abundant species within the Salish Sea and the focus of many ongoing monitoring efforts. *M. pyrifera* is less common and is mostly restricted to exposed shores along the Strait of Juan de Fuca (Pfister et al. 2018). These species occur throughout the

California Current Large Marine Ecosystem and are found on the outer coasts of Washington and British Columbia, as well as in the inland waters of the Salish Sea. Kelps are found in high current areas, like the Tacoma Narrows, throughout Admiralty Inlet, and along the Strait of Juan de Fuca. In addition to the canopy-forming kelps, numerous understory kelp species are abundant in subtidal areas of the Salish Sea.

Kelps serve several ecological functions and provide habitat and nutrients to numerous species. For example, they affect their physical environment by modifying current and wave energy, contribute to carbon cycling and storage via large algal fronds, and they facilitate nutrient exchange (Hurd et al. 2014). Kelps also contribute to local biodiversity and feed herbivores with their high rates of primary production (Teagle et al. 2017). Kelps support a wide array of flora and fauna,

from epiphytes that attach to the kelp's stipes and blades, to fishes that use surface and subtidal canopies of kelp as refuge. The kelp crab (*Pugettia producta*) is an especially common associate that eats kelp and other animals associated with kelp, such as mussels, barnacles, and crustaceans. It is likely that these crabs also provide food for fishes and mammals that utilize the kelp canopy, but few studies have been done in this region (see Zuercher & Galloway 2019 for a general discussion). Multiple species of fish use kelp forests as habitat, including rockfish, juvenile salmon, and herring which spawn on the kelp blades (Schweigert et al. 2018) and provide a food source for Indigenous peoples (Gauvreau et al. 2017).

Trends in kelp cover in the Salish Sea are variable, but no transboundary monitoring effort exists across the seascape. In the Strait of Juan de Fuca and more exposed areas, kelp canopy cover

had remained stable or increased (Berry et al. 2005) until recently when reductions in cover were observed (Shelton et al. 2018). In the South Puget Sound, recent monitoring showed a decline in *Nereocystis* in many areas, but stable cover persisted around the Tacoma Narrows, which is an area of high current and tidal exchange (Berry et al. 2019; Berry et al. 2021). In British Columbia, most work focuses on the west coast of Vancouver Island, but recent research using remote sensing shows a decline in kelp abundance in the Salish Sea around Cowichan Bay and Sansum Narrows in recent years (Schroeder et al. 2020). Studies aimed at identifying mechanisms related to these declines are ongoing in both Washington and British Columbia, but time-series with broad spatial coverage are needed to adequately assess long-term trends and separate them from annual or shorter-term variability in kelp canopy cover and species diversity.



Large bull kelp bed in Puget Sound
Photo: Rich Yukubousky

Glass Sponges

Glass sponges form unique reef ecosystems found along the Pacific coast of Canada and the United States. Similar glass sponge reefs went extinct during the age of the dinosaurs, but modern versions were discovered in Hecate Strait in central British Columbia in the mid-1980s and have become the subject of more recent research in the Strait of Georgia and the ocean waters off of Washington, British Columbia, and north to Alaska. Sponge reefs in the Salish Sea have been found in Howe Sound, around the Gulf Islands, and in the Strait of Georgia. Perhaps surprisingly, no records of glass sponge reefs exist for Puget Sound. Most reefs are found in very deep waters, greater than 150 m (492 ft), which is beyond the range of SCUBA. As remotely operated vehicle (ROV) and autonomous underwater vehicle (AUV) technology has become more available, exploration and study of these habitats has become possible. Recent work in the Strait of Georgia has identified their role in the northern Salish Sea (Kahn et al. 2015), and management actions like designating reefs as marine protected areas have ensured protection of these habitats.

Glass sponges form reefs similar to tropical corals, where successive generations build upon existing sponge structures. The oldest parts of the reef are cemented together and buried by sediments, forming bioherms. Using scaffolding made of silica, the bioherms formed can be extensive, spanning hundreds of square kilometers and reaching heights of 20 meters or more (66 feet or more). In the Strait of Georgia, the reefs are smaller than in Queen Charlotte Sound and along the northwest coast. The reefs are generally very old, with estimates dating to over 9,000 years in some places (Krautter et al. 2001) and over 200 years in the Strait of Georgia. There are two main species that form the glass sponge reefs of the Salish Sea: the vase sponge (*Heterochone calyx*, sometimes called goblet sponge) and the cloud sponge

(*Aphrocallistes vastus*). A third species (*Farrea occa*) is found in northern coastal reefs.

Because the reefs are only found in the northeastern part of the Pacific Ocean, it is believed they require very specific conditions to form. For example, cold water, low light, and high dissolved silica concentrations are all key to colonization and expansion. Levels of dissolved silica are especially high in waters off the Pacific Northwest and because >90% of a glass sponge's body structure is made of silica, it is critical for the growth of the organism and the reefs. Water temperatures at depths where reef-building glass sponges live are between 6°C and 12°C (43°F and 54°F). When glass sponges are exposed to temperatures outside this range they lose their ability to control how they pump water through their colonies, which is their primary means of feeding and waste removal.

Little light reaches the sponge reefs, as most are found below the photic zone where primary productivity occurs. One explanation for the lack of sponges in Puget Sound is the need for hard substrate for recruitment of larvae; the mostly soft-bottom substrates found in Puget Sound are not conducive to settlement (P. Johnson, University of Washington, personal communication). Sedimentation also has a key role in affecting sponge health and reef formation. For the bioherms to form, clay sediments are required to bury and cement the foundation of the reef, but excess sedimentation can smother and kill the live sponges. Puget Sound sees higher sedimentation than many parts of the Strait of Georgia; this may prohibit growth, although sponges can survive in elevated and sheltered parts of the seafloor. For example, live sponges are found on the leeward side of a submarine ridge in front of the Fraser River plume (Chu & Leys 2010).

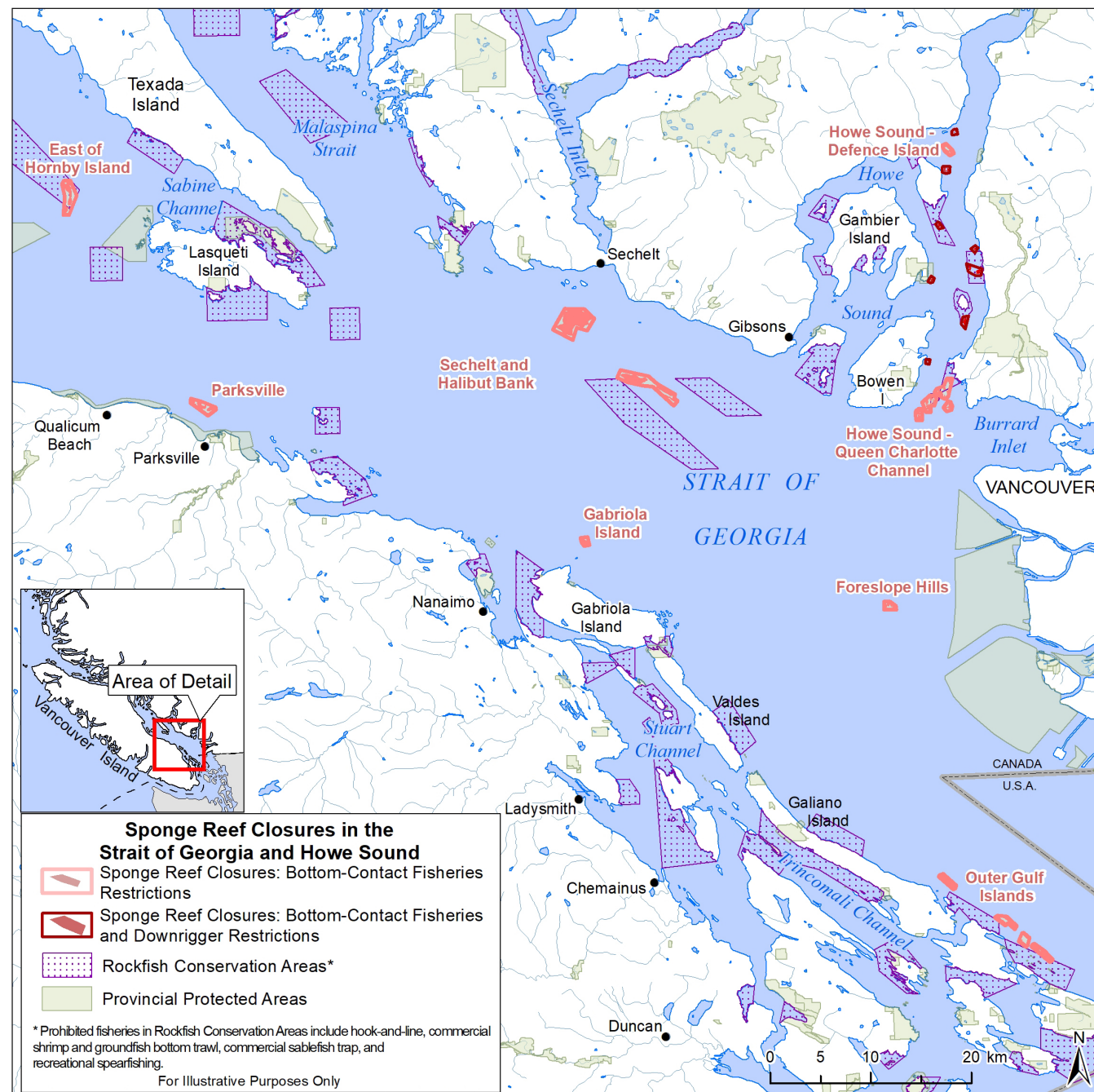
The reefs contribute to the productivity of benthic ecosystems by forming complex habitat for diverse communities of invertebrates and fish. Surveys have shown over 100 species of fishes and invertebrates to be associated with glass sponge reefs, including rockfish (both juveniles and adults), shrimp, crabs, and other benthic organisms (Marliave et al. 2009; Chu & Leys 2010; Stone et al. 2013; Dunham et al. 2018). The reefs also play an important role in nutrient cycling. Glass sponges are efficient filter feeders removing up to 90% of bacterial cells from seawater they filter, and collectively, reefs can filter about 1% of the total water volume in the Strait of Georgia and Howe Sound daily, despite covering only <0.2% of the area of the seafloor (Dunham et al. 2018). Recent research has focused on the role of glass sponge reefs in carbon cycling, finding that they can remove up to 1 gram of carbon per square meter (g C/m²) daily, which is impressive and comparable to terrestrial old growth forests and kelp forests (Dunham et al. 2018). As one of the densest known communities of deep-water filter feeders, this is one example of how glass sponge reefs link benthic and pelagic environments through nutrient (carbon and nitrogen) cycling. Because of their immense size and long-lived nature, the sponge reefs act as regionally important sinks of silicon and carbon (Chu et al. 2011; Kahn et al. 2015).

The uniqueness and fragility of these biogenic systems makes them susceptible to climate change and anthropogenic habitat loss. Recognizing that a better understanding of glass sponge reefs is needed and that trawling and other benthic disturbances threaten these important habitats, Fisheries and Oceans Canada has established a marine protected area encompassing the four largest reefs in Hecate Strait and has closed fisheries on 17 reefs in Howe Sound and the Strait of Georgia



Glass sponge at the Galiano reef in the Salish Sea. Source: Jackson Chu, University of Victoria.

(Figure 2.9). These bottom-contact fishing closures have been in place since 2015, with the official conservation boundaries formalized in 2018. Ongoing research aims to address glass sponge trophic ecology, carbon sequestration potential, and other ecosystem functions. Meanwhile, recognizing glass sponge reefs as important biogenic habitats and protecting them by designating additional marine protected areas will contribute to their persistence, health, and perceived ecosystem value.



Above: Figure 2.9. Sponge reef closure designations in the Strait of Georgia and Howe Sound. Source: Fisheries and Oceans Canada (2021).

Right: Olympia oysters growing on a Pacific oyster shell
Photo: Cheryl Lowe

Oysters

Olympia oyster (*Ostrea lurida*) is the only species of oyster native to the Pacific Coast of North America and the Salish Sea. Olympia oysters were once an important food source for Indigenous peoples (Arima 1983; Batdorf 1990) and, prior to European settlement, dense assemblages of Olympia oysters covered much of the Salish Sea's intertidal zone (Norgard et al. 2018). The Pacific oyster (*Crassostrea gigas*), a non-native species, is more commonly known because it is a commercial product produced by many shellfish growers in the Salish Sea; it was introduced as a faster growing alternative to the Olympia oyster when overfishing decimated native oyster stocks by the early 1900s (Steele 1957). Siltation from large-scale forestry operations and contamination from industry also contributed to decline of the Olympia oyster. Despite these obstacles, Olympia oyster (or native oyster) populations are resurging, and restoration efforts are underway in both Washington and British Columbia waters (see Vignette 4, Olympia Oysters).



Olympia oysters are found in estuaries, saltwater lagoons, tidal flats, and protected areas such as pocket beaches. They live lower in the intertidal zone than Pacific oysters, making them less visible to beachcombers. Like other bivalve mollusks, such as clams, geoducks, mussels, and scallops, oysters are filter feeders, filtering water and particulates (including phytoplankton and zooplankton) throughout the Salish Sea. Compared to the Pacific oyster, Olympia oysters are small, relatively flat, and usually less than 60 mm (2.4 in) in length. Olympia oysters are also well-adapted to upwelling environments, making them more resilient to ocean acidification (Waldbusser et al. 2016). In fact, experimental studies showed temperature and salinity to be more important than ocean acidification in determining larval success (Lawlor & Arellano 2020).

Although populations of Olympia oyster remain relatively small compared to other bivalve species, restoration of this once important native species (and maintenance of shellfish more broadly) is important to the overall health and functioning of the Salish Sea (White et al. 2009; Norgard et al. 2018). Beyond their helpful ability to filter large amounts of water and provide many other ecosystem services, oysters and other shellfish are important cultural and economic resources (Coen et al. 2011). However, these same beneficial attributes make oysters and other shellfish sensitive to natural and anthropogenic change, meaning they serve as important sentinels of change in the Salish Sea. For example, water temperature, ocean acidification, contaminants, and siltation all impair functional shellfish beds, indicating that ongoing monitoring efforts in both Canada and the United States are important, even if most studies are aimed at public health objectives in relation to shellfish harvesting rather than a broader ecological context.

BIOPHYSICAL CONNECTIVITY ACROSS THE SALISH SEA ECOSYSTEM

As discussed above, the intersection and coupling of biogenic habitats with the dynamic and nutrient-rich pelagic environment is partly what makes the Salish Sea such a productive estuarine ecosystem. As in many estuaries, the connectivity within the system is facilitated by filter feeders (e.g., oysters and glass sponges), while primary producers (e.g., eelgrass and kelp) convert nutrients into biomass and create habitats that in turn support numerous fish and invertebrate species. Through physical movement and trophic interactions, these species then transport organic matter from highly productive, shallow, photic zone habitats to deeper benthic or pelagic habitats within the Salish Sea.

While kelp and eelgrass habitats represent only a small proportion of the estuarine area in the Salish Sea, their importance in the food web and overall productivity in the ecosystem is assumed to be much greater (Mumford & Thomas 2007). Similarly, glass sponge reefs represent a very small proportion of area in the Salish Sea, but their function in carbon cycling is considerable (Dunham et al. 2018). The structure and protection these habitats provide for myriad species helps maintain ecosystem coupling and healthy ecosystem services. Their conservation is necessary for ecosystem function and resilience and monitoring their populations will be necessary to detect change (Loh et al. 2019).

Understanding the connectivity of organisms and habitats in this region continues to develop (Gaydos et al. 2009). Once considerable migrations of Pacific salmon with diverse life-histories brought marine-derived nutrients to watersheds (Ben-David et al. 1998; Gustafson et al. 2007). But the diminished runs of Pacific salmon (Bradford & Irvine 2000), especially Chinook and coho salmon, are one example of reduced connectivity between the estuary and watersheds, in this case the connectivity of both adults migrating landward and juveniles migrating seaward (Scheuerell et al. 2011). Within the estuary, organisms like shorebirds and juvenile salmon use shallow, productive tide flats like Padilla Bay, Washington, or Roberts Bank, British Columbia, to feed locally before moving to other habitats (Condon et al. 2013; Luxa 2013). The movement of birds, mammals, and fishes, and the physical transport of material (e.g., sediments, nutrients, carbon) from the surrounding watersheds, through the Salish Sea ecosystem, and out to the continental shelf and beyond makes it clear that the Salish Sea contributes to—and is reliant upon—a truly vast spatial scale.



*Scientist measuring eelgrass bed
Photo: Ronald Thom*

01 | THE SALISH SEA ESTUARY SYSTEM

Dr. Bert Webber, Senior Fellow, Salish Sea Institute

The entirety of the Salish Sea is an estuarine ecosystem. Nested within the larger Salish Sea watershed, this estuarine ecosystem is the source of the rich biological structures and functions that make the Salish Sea of particular interest. It is the place where the freshwater from land drainages mixes with the waters of the Pacific Ocean and results in water with a measurable, although sometimes small amount of freshwater. One of the Salish Sea's unique characteristics is that in most places the water is quite salty. The Pacific Ocean off the Washington coast is around 34 PSU (practical salinity units, how salinity in water is measured), while most places in the Salish Sea have a surface salinity only a bit less—around 29 PSU. To most people's taste, this water would seem as salty as the ocean, but it is still a genuine estuary, where seawater is diluted with freshwater.

The Salish Sea is among the preeminent estuaries of North America, such as San Francisco Bay, the Florida Everglades, Chesapeake Bay, the St. Lawrence River, and Bristol Bay to name a few. All of these estuaries share the characteristic of high biological productivity. Estuaries are four times more productive than terrestrial grasslands, are twenty times more productive than the open ocean, and rival the most productive terrestrial crop, sugar cane, in terms of biological productivity. Like forests, grasslands, and intensively cultivated agriculture lands, estuaries produce high amount of organic material.

The food webs—pelagic, demersal, and nearshore—are diverse and rich. In the water of the estuary there is an abundant and complex array of species. The foundation of the pelagic zone is the photosynthesis of microscopic organisms—the phytoplankton. They create the food source that sustains the animal life, including the species we value as food, like the forage fish, and the larger species of fish, like salmon and rockfish. As well, many bird and mammal

species depend on this complex food web. Near the shorelines the estuary supports rich beds of seagrasses and kelps, species with high value as habitat for many animal species.

We have known for some time (the 1970s and 1980s work of Curtis Ebbesmeyer and others) that there is a two-way circulation of waters in the Salish Sea. Surface waters move towards the ocean, and deeper waters move from the ocean into the Salish Sea. The movement is subtle and cannot be easily detected looking at the surface of the water on timescales in which we might make casual observations.

What causes the estuarine circulation? As the water from a river flows over the surface of the estuary, it moves seaward, pushed by the incoming river flow. As the freshwater moves across the surface of the estuary, the friction between the river flow and estuary below causes the deeper water to be pulled towards the surface, a process called entrainment. In a flat bottom estuary like Chesapeake Bay, entrainment continually pulls saltier water from below, and the salinity of surface water increases. In the absence of any other disturbance like wind, entrainment continues until the water is well-mixed and uniform.

The Salish Sea is different. Because of the irregular bathymetry, there are locations with active tidal currents where the water is agitated from surface to bottom. In these "washing machine" areas, water is vigorously mixed from surface to bottom, and surface water salinity increases. This is the mechanism that results in the surface water of the Salish Sea being so salty. Once through the tidal currents, the estuarine circulation is restored, with saltier water on the bottom and fresher water at the surface, and the journey to the mouth of the estuary continues.

So how much water is involved with the estuarine flow? The annual discharge of Salish Sea rivers allows us to calculate the total annual estuarine flow. The amounts are immense. Estuarine scientists have determined the entrainment of deeper water by the pushed surface water is between 10 and 20 times the river flow. This mixing of the rivers' freshwater and the deep Pacific Ocean water creates an immense movement of surface water towards the ocean mostly via the Strait of Juan de Fuca. A conservative estimate indicates that the amount of the outward estuarine flow from the Salish Sea through the Strait of Juan de Fuca is equal to a value that is eight times the annual flow of the Columbia River.

This freshwater flow drives estuarine circulation throughout the Salish Sea. We know that the replacement time of the total water of Puget Sound (the residence time) is around 3-6 months. That is, the

volume of Puget Sound is replaced about three times a year by estuarine circulation. The outgoing estuarine flow is replaced by higher salinity, nitrogen-rich ocean water entering the Salish Sea at depth. This inflow works its way into all parts of the Salish Sea, providing the relatively high values of biological nitrogen that fuel the productive ecosystem.

While most of the biological nitrogen originates from the ocean waters, high concentrations of biological nitrogen remain in the outflow as well, stimulating primary productivity of ocean surface waters off Vancouver Island and the northwest coast of Washington.

The nature of this circulation, the rich biological systems dependent of the flow, and the resilience of the freshwater sources that drive estuarine flow are central to the Salish Sea Ecosystem.



The Salish Sea from space
Photo: NASA 2021

02

LOWER TROPHIC LEVELS IN THE SALISH SEA: RECENT FINDINGS FROM THE STRAIT OF GEORGIA

Dr. Ian Perry, Pacific Biological Station, Department of Fisheries and Oceans

Plankton form the base of the pelagic marine food web in the Salish Sea, and are eaten by fishes, marine mammals, and seabirds. Plankton include microscopic plants (phytoplankton) and very small animals (zooplankton). They drift in the water but can accumulate in very large numbers as a result of water currents, and growth and reproduction. In the Canadian waters of the Salish Sea (including the Central and Northern Strait of Georgia, and the Strait of Juan de Fuca), diatoms (which are single-celled algae that have a cell wall of silica) make up most (over 90%) of the phytoplankton during spring, but in the summer the phytoplankton are composed of a greater variety of species, in particular of small flagellates (which have cell walls composed of cellulose). Autumn has the greater diversity of phytoplankton species, with a mixture of flagellates remaining from the summer and diatoms beginning to grow again when storms mix nutrients back into the surface layers of the Strait (Nemcek et al. 2020).

Chlorophyll a is the main pigment in plants (it makes them green) and is used as a measure of the amount (or biomass) of phytoplankton. Seasonally, chlorophyll a in the Strait of Georgia is lowest during the winter when there are lots of nutrients but plant growth is limited by low light levels, highest during the spring when nutrients and light are optimal for growth, low during summer when nutrients are low, and higher again with episodic blooms during the autumn caused by wind events, which replenish the nutrients in the upper water layers (Figure 1, Suchy et al. 2019).

Phytoplankton chlorophyll concentrations have been monitored by satellites since 2003 and have been used to understand year-to-year changes in the amount of phytoplankton in the Strait of Georgia (Suchy et al. 2019). Moderate to high concentrations

of chlorophyll a occurred in this region in 2005 and 2015, concurrent with early and strong flows of freshwater from the Fraser River into the Strait of Georgia, and with low numbers of windstorms. Chlorophyll a in the Northern Strait of Georgia over the period 2003 to 2016 was related to the temperature at the surface of the water and to the amount of light available for the plants to grow (which varies among years depending on cloud cover). In the Central Strait of Georgia over this same time period, Chlorophyll a concentrations were related to the amount of freshwater flowing from the Fraser River. All of these physical processes (sea temperature, amount of light for growth, and freshwater from the Fraser River) control the extent of vertical mixing in the Strait of Georgia, which in turn controls the amount and types of phytoplankton that grow in the Strait during the year. The median Chlorophyll a concentration in the Northern Strait of Georgia is also related to several atmosphere/climate indices, such as the Pacific Decadal Oscillation, but not in the Central Strait. This suggests that phytoplankton dynamics in the Central Strait of Georgia are more strongly influenced by local factors, such as flow from the Fraser River. While Chlorophyll a is an indicator of phytoplankton biomass, it does not tell the entire story of phytoplankton production because much of the phytoplankton is consumed by zooplankton.

Zooplankton are the small animals that largely feed on the phytoplankton, and in turn are eaten by other zooplankton, fishes, marine mammals, and seabirds. They have been monitored consistently in the Central and Northern Strait of Georgia since 1996 (Mackas et al. 2013). Total zooplankton biomass was highest in the late 1990s, then declined quickly to a minimum in 2005, and has recovered since 2010 to above normal

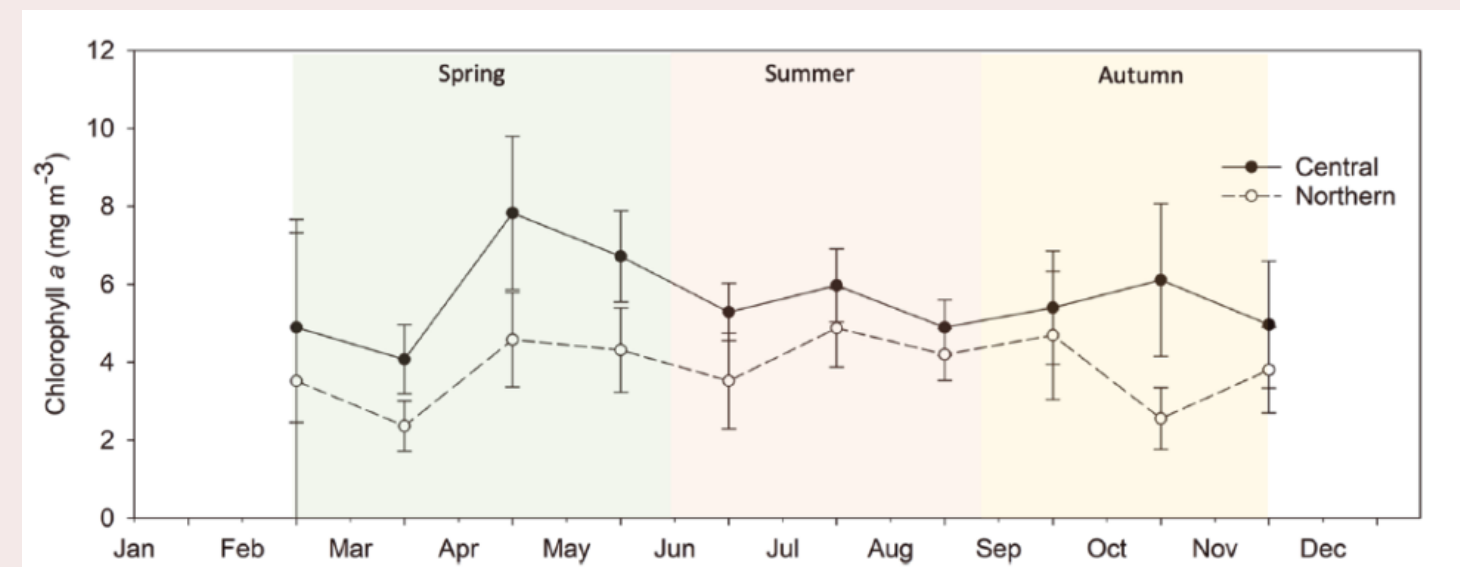


Figure 1. Typical pattern of monthly chlorophyll a concentrations in the Central and Northern regions of the Strait of Georgia as determined from weekly satellite remote sensing from 2003 to 2016. Vertical bars represent the 95% confidence intervals about the monthly mean values. Source: Reproduced from Suchy et al. (2019).

biomass levels (Figure 2; Perry et al. 2021). Most (76%) of the biomass of zooplankton are composed of four types of animals: medium and large copepods, euphausiids, and amphipods. Interannual changes in zooplankton biomass over this period were related to the salinity at the sea surface, the timing of the bloom of phytoplankton during the spring, and the Pacific Decadal Oscillation (a large-scale climate index).

Zooplankton abundance is important for the marine food web, and variations in the types of zooplankton and their abundance can impact growth and survival of fishes. Statistical models that included salinity, sea temperature, freshwater flow from the Fraser River, and the wind over the sea surface (all of which control the vertical mixing of the water column and the circulation in the Strait of Georgia), as well as zooplankton biomass, explained much (38-85%) of the interannual variability of the early marine survival rates of three populations of Chinook salmon in the Canadian waters of the Salish Sea. However, these analyses were based on conditions that occurred from 1996 to 2018; if climate change pushes conditions outside of those observed during this period, these statistical relationships may break down. Climate change—and the resulting change in river flow, temperature, or wind patterns—may lead to unusual and unexpected patterns of phytoplankton

and zooplankton, which in turn could affect early marine Chinook salmon survival and the growth and development of other zooplankton-eating organisms.

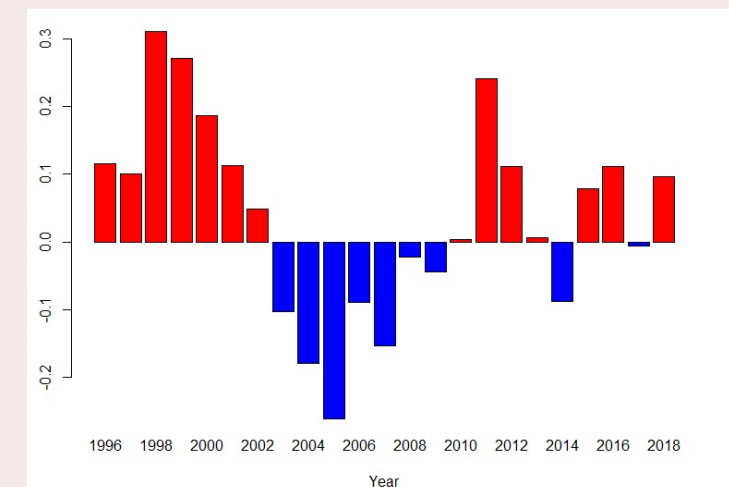


Figure 2. Total zooplankton biomass in Central and Northern Strait of Georgia, 1996 to 2018 (values shown are 'anomalies' or differences from the average values between 1996 to 2010). Source: Modified after Perry et al. (2021).

03 | BIRDS OF THE SALISH SEA

Dr. Rob Butler, Pacific WildLife Foundation

The Salish Sea—the largest inland sea on the west coast of Canada and the United States—supports jobs, supplies food, attracts tourists, provides recreation, is the basis of Indigenous cultures, and provides ecosystem services. Millions of people reside along its shores, and thousands of jobs are connected to the Salish Sea. Tourism and recreation related to bird watching and whale watching is a growing market. The Salish Sea is the ancestral home to Indigenous people whose ancient culture is connected to birds and mammals. The presence and abundance of birds and marine mammals indicates a healthy ecosystem and establishes a baseline for recovery. To sustain these animals and all they provide to us requires saving their homes, halting persecution, and preventing pollution of their food.

The significance of the Salish Sea comes into focus when we look at the diversity and abundance of its birds and mammals, some of which are globally, continentally, and nationally important. Of particular importance is the diversity and abundance of species on the Fraser River Delta. There are more species of birds on the delta than any comparable area in Canada, and nearly half of all 550 species of birds reported for British Columbia have been seen on the delta. Maximum single day counts for all species tallies to about 2 million birds, and the number that pass through on migration is several times greater. For example, over a million shorebirds migrate across the delta and through the Salish Sea annually, and hundreds of thousands of waterfowl spend their non-breeding season there.

Other areas in the Salish Sea attract large numbers of birds and marine mammals. When Pacific herring spawn on the east coast of Vancouver Island in late winter and early spring, tens of thousands of seabirds and seaducks, and hundreds of sea lions assemble to feed on fish and eggs. Channels and passages with

high tidal flow can draw thousands of gulls. Whales from Hawaii and Mexico and seabirds from across the Pacific assemble in large flocks at the western entrance to the Strait of Juan de Fuca.

Among the 172 species of birds that use the waters of the Salish Sea each year (Gaydos & Pearson 2011) are waterfowl, loons and grebes, seabirds, herons, birds of prey, and shorebirds, whose collective annual ranges encompass the area bounded by Siberia, the Canadian High Arctic, Florida, and Peru.

Commonly encountered waterfowl in estuaries with agricultural lands in winter are the snow goose, trumpeter swan, American wigeon, northern pintail, green-winged teal, and mallard. Rocky shores yield thousands of surf scoters and Barrow's goldeneyes, and four Pacific Northwest endemic shorebirds: the black turnstone, black oystercatcher, surfbird and rock sandpiper. In spring and summer, mudflats are frequented by over 50 species of shorebirds, including hundreds of thousands of western sandpipers, and some rocky islands support a breeding cadre of Pacific Northwest species such as glaucous-winged gull, pelagic cormorant, pigeon guillemot and black oystercatcher. Late summer brings post-breeding common murrelets, Heermann's, Bonaparte's, and mew gulls. Ancient murrelets enter the Salish Sea in autumn and marbled murrelets spend the winter there. Killer whales come in search of salmon and marine mammals as prey, harbour porpoise, white-sided dolphins, and humpback whales seek schools of small fish, and gray whales plough up mudflats in pursuit of marine invertebrates.

The diversity and abundance of birds and marine mammals is built on an ecological foundation of marshes, mudflats, rocky shores, mixing of ocean currents, tides, and river flow that provide plankton, fish, and plants as food. High densities of plankton



*A bald eagle takes off from tree branch
Photo: Taylor Bayly*

occur off the Fraser River plume, serving as food for herring, sandlance, and anchovy that are eaten by diving birds, gulls, and marine mammals; biofilm forms on estuarine mudflats supplying energy needs for migrating sandpipers; eelgrass growth in spring provides a nursery for small fish for diving birds; and mussels and other marine invertebrates feed the large numbers of seaducks.

The abundance and diversity of marine birds and mammals has led to conservation initiatives to safeguard their presence. Twenty-two areas in the Salish Sea have been designated as Important Bird and Biodiversity Areas, of which the Fraser River Estuary has the greatest number of global, continental, and national species in Canada. Waters in the southern Strait of Georgia and the Strait of Juan de Fuca have been identified as an Important Cetacean Area for gray and humpback whales and critical habitat for endangered southern resident killer whales.

Despite all that has been learned about marine birds and mammals, large areas of the Salish Sea in Canada have not been systematically surveyed. The Salish Sea Marine Bird and Mammal Atlas is a project led by the Pacific WildLife Foundation with our partner Birds Canada, aimed at systematically mapping the distribution of marine birds and mammals in the Canadian waters. The atlas project used standard protocols to survey birds along the shore and at sea. The atlas will combine three decades of land-based bird surveys in Birds Canada's Coastal Waterbird Survey with surveys at sea led by Pacific WildLife Foundation. The atlas will be available online as an Esri storymap with links to technical reports and raw data of at sea surveys and the Coastal Waterbird Survey. The data will be useful for environmental assessments, sea level rise impacts, and tourism and recreation planning, and will serve as a baseline to measure change in the future.

04 | OLYMPIA OYSTERS

Dr. Jodie Toft and Betsy Peabody, Puget Sound Restoration Fund

Olympia oysters (*Ostrea lurida*) are our only native oyster species here in the Salish Sea. The namesake of Washington State's capital and a sought-after delicacy for miners during California's Gold Rush, Olympia oysters once covered an estimated 13-26% of the intertidal area in Puget Sound, mostly near the heads of inlets. A combination of overharvest, pollution, and habitat loss reduced the current population to less than 4% of historic numbers, though sparse numbers of Olympia oysters can still be found throughout most of their historic distribution. Looking to the future, as our region's marine waters experience effects of climate change and ocean acidification (OA), native species such as the Olympia oyster may prove to be a critical building block in overall resilience of the marine ecosystem. Not only do Olympia oysters provide a suite of ecosystem services including water filtration and creation of intertidal habitat structure, but they may have adapted over the eons to cope with wide fluctuations in the pH of Puget Sound, possibly making them hardy to OA-induced stress. In experiments conducted at Oregon State University, Olympia oyster larvae have shown themselves to be more tolerant to low pH levels than non-native Pacific oysters, perhaps due to Olympia oysters' relatively slow development (Waldbusser et al. 2015). By bringing back what was once abundant—our small but mighty Olympia oyster—we may also be bringing a more reliable stream of benefits that they provide—including improved water quality and local food—as they (and we) weather changing ocean conditions.

Olympia oyster restoration in Puget Sound has been underway since 1999. It has grown into a sustained priority for state, federal, tribal, and nonprofit partners working to improve the health of the Salish Sea. Puget Sound Restoration Fund (PSRF), a local non-profit dedicated to restoring

foundational elements of Puget Sound's marine ecosystem, and many other partners have been restoring Olympia oysters in Puget Sound in several of 19 priority locations. Those locations are described in Washington Department of Fish and Wildlife's 2012 updated Olympia oyster stock rebuilding plan. The 19 sites are locations where Olympia oyster populations were once abundant and also sites that, once populations are restored, may serve as source populations, spilling over to repopulate other areas of Puget Sound.

The main methods for restoration are to add settlement substrate to areas where Olympia oyster larvae are found, and to distribute oyster seed as spat-on-shell or individual oysters. For the first method, the substrate most often used is clean Pacific oyster shell, which is distributed over the restoration site to provide habitat for Olympia oyster larvae to settle on. The second tool in the restoration toolbox is to distribute restoration-grade Olympia oyster seed as spat-on-shell or small, individual oysters across the restoration site. Spat-on-shell, as the name indicates, refers to small Olympia oysters that have settled onto Pacific oyster shells, which provide structure for the settlement of larval Olympia oysters. It turns out, Olympia oysters love the rough, craggy surface Pacific oyster shell provides. The bags of shell are then delivered to restoration sites, opened and spread across the area of interest. In areas without breeding populations, reintroduction of Olympia oyster seed serves as a jump start for the population. Spat-on-shell production happens either by catching Olympia oyster larvae in the wild or producing them in a conservation hatchery. If in the wild, bags of Pacific oyster shells are placed within the basin of interest in areas where monitoring has shown Olympia oyster larvae to be abundant. If larvae successfully settle, the spat-on-shell bags are then relocated to the restoration site. Alternatively,

adult broodstock oysters are collected in the wild, from within the same basin as the prospective restoration site, and brought to a conservation hatchery, where larvae are produced and settled onto bags of shell following conservation genetic protocols. A key element of this strategy is having a conservation hatchery (or following conservation protocols within alternative settings).

In 2014, PSRF, the National Oceanic and Atmospheric Administration (NOAA) and other partners took a bold step forward for Olympia oyster restoration by establishing the Kenneth K. Chew Center for Shellfish Research and Restoration, which PSRF operates at NOAA's Manchester Research Station. The Chew Center is dedicated to research and production of native shellfish and other Pacific Northwest living marine resources. The development of a conservation hatchery was identified as a high-level need in both phases of the Washington Shellfish Initiative, as guided by the National Shellfish Initiative, and as a recommendation of the Blue Ribbon Panel on Ocean Acidification in the 2012 and 2017 reports. The facility is operated through a cooperative research and development agreement (CRADA) between NOAA and PSRF. With the Chew Center up and running, PSRF and partners could accelerate the pace of restoration and continue to ensure that restoration-grade spat-on-shell were produced, with genetic fidelity to the basins in which restoration was to take place. The collaboration was further solidified in 2017, when the state began providing base-level funding to cover 50% of hatchery operations through the Washington State Department of Fish and Wildlife.

The capacity to produce Olympia oysters for priority locations also supported an ambitious goal, set in 2010, to restore 100 acres of Olympia oyster habitat by the end of 2020, in partnership with multiple stakeholders. We successfully reached the restoration goal in 2020, buoyed by restoration in Sinclair Inlet, Liberty Bay, Port Gamble Bay, Fidalgo Bay, Dyes Inlet, and many other locations. The work is highly collaborative in nature, with partnership and support from a dizzying array of groups, including Washington State Departments Fish and Wildlife, Ecology,

and Natural Resources, the Suquamish Tribe, the Swinomish Indian Tribal Community, the Jamestown S'Klallam Tribe, the Port Gamble S'Klallam Tribe, the Squaxin Island Tribe, the Skokomish Tribe, the Nisqually Indian Tribe, the Samish Indian Nation, the Tulalip Tribe, Northwest Straits Commission and Marine Resource Committees, NOAA, shellfish growers, tideland owners, University of Washington, and United States Department of Agriculture's Natural Resources Conservation Service. To put this collective accomplishment into perspective, only 150 acres of natural, dense Olympia oyster beds were estimated to exist in 2010.

In recent years, restoration of Olympia oysters has expanded and taken hold beyond the Salish Sea. In California, Oregon, and British Columbia, groups have been working to bring back assemblages of the West Coast's native oyster, building from lessons learned in Puget Sound, as well as early seeding efforts in Oregon in the mid-1990s. The group of oyster conservation and restoration practitioners that has developed on the West Coast is known formally as NOOC—the Native Olympia Oyster Collaborative. For the curious among us, NOOC has recently launched a story map to showcase nearly 40 Olympia oyster restoration projects, distill findings, and serve as a powerful and collective communication tool.

The success story of the return of Olympia oysters is beginning to unfold. The truth is that they have been here all along, just hidden away in small numbers—present, not abundant, yet a persistent part of our nearshore ecosystem. As this once high-profile species makes its way back into our region's conversations, it reemerges as part of our culture. And as we rebuild low density aggregations into complex, three-dimensional habitat, we rebuild a fundamental part of our marine ecosystem, one that supports fish, invertebrates, and ultimately, one that supports us.