Appendix A: Kelp Knowledge Review

A.1 Kelp Biology and Ecology

The term "kelp" broadly refers to large (10 cm to 30 m) brown macroalgae (class Phaeophyceae) of the order Laminariales that form complex three-dimensional habitats in shallow, nearshore waters (Dayton 1985). Worldwide, the Laminariales consist of approximately 147 different species, including *Laminaria* spp., *Saccharina* spp., and iconic canopy-forming species such as *Nereocystis luetkeana* (hereafter *Nereocystis*) and *Macrocystis pyrifera* (hereafter *Macrocystis*) (Druehl and Clarkston 2016; Teagle et al. 2017). Kelp can be annual or perennial depending on the species.

Washington State is home to 22 species of kelp. These kelp species come in three different forms: *Prostrate kelp*, which lack a rigid stipe or gas-filled buoy, remain close to the seafloor, forming thick understories; *stipitate kelp*, which stand erect and form a subcanopy of kelp in the water column; and *floating kelp*, which rely on gas-filled pneumatocysts to suspend them in the water column and can create large, floating surface canopies. Prostrate kelp species are the most commonly distributed kelp species in Puget Sound. Table A-1 identifies the kelp species found in Washington State and provides associated taxonomic synonyms, common names, places of location, and forms.

Table A-1. Washington State Kelp Species.

Species Name	Taxonomic synonyms	Common name	Washington State Waters	Kelp Recovery plan study area	Form
Agarum clathratum Dumortier	*A. cribrosum*	-	X	X	prostrate
Costaria costata (C. Agardh) D.A. Saunders	-	-	X	X	prostrate
Dictyoneurum californicum Ruprecht	-	-	X	-	prostrate
Dictyoneurum reticulatum (D.A.Saunders) P.C.Silva	*Dictyoneuropsis reticulatum*	-	X	-	prostrate
Neoagarum fimbriatum (Harvey) H.Kawai & T.Hanyuda	*Agarum fimbriatum*	-	X	X	prostrate
Alaria marginata Postels et Ruprecht	*incl. Alaria nana*	-	X	X	prostrate
Lessoniopsis littoralis (Farlow et Setchell ex Tilden) Reinke	-	-	X	-	stipitate
Pleurophycus gardneri Setchell et D.A. Saunders ex Tilden	-	-	X	X	prostrate
Pterygophora californica Ruprecht	-	-	X	X	stipitate

Species Name	Taxonomic synonyms	Common name	Washington State Waters	Kelp Recovery plan study area	Form
Egregia menziesii (Turner) Areschoug	-	feather boa kelp	X	X	floating
Hedophyllum nigripes (Rosenvige) Starko, S.C.Lindstrom & Martone	*	-	X	X	prostrate
Hedophyllum sessile (C. Agardh) Setchell	*Saccharina sessilis*	sea cabbage	X	X	prostrate
Macrocystis pyrifera (Linnaeus) C. Agardh	*Macrocystis integrifolia*	giant kelp[1]	X	-	floating
Nereocystis luetkeana (Mertens) Postels et Ruprecht	-	bull kelp	X	X	floating
Postelsia palmaeformis Ruprecht	-	sea palm	X	-	stipitate
Saccharina complanata (Setchell & N.L.Gardner) P.W.Gabrielson, S.C.Lindstrom & O'Kelly	*Laminaria complanata*	-	X	X	prostrate
Saccharina latissima (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders	*Laminaria saccharina*	sugar kelp	X	X	prostrate
Cymathaere triplicata (Postels et Ruprecht) J. Agardh	*Laminaria triplicata*	-	X	X	prostrate
Laminaria ephemera Setchell	-	-	X	X	prostrate
Laminaria longipes Bory	-	-	X	X	prostrate
Laminaria setchellii P.C Silva	*Incl. L. dentigera*	-	X	X	stipitate
Laminaria sinclairii (Harvey ex Hooker f.) Farlow, C.L. Anderson et D.C. Eaton	-	-	X	X	prostrate
Total	-	-	22	17	-

* *Saccharina nigripes, Saccharina groenlandica, Saccharina subsimplex, Laminaria groenlandica, Laminaria bongardiana, Laminaria bullata f. subsimplex.*

A.1.1 Kelp Life History

All kelp exhibit heteromorphic life histories of alternating generations (Hurd et al. 2014). Kelp alternate between a large, asexual, diploid, macroscopic form called a sporophyte and microscopic,

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[1] Giant kelp (*Macrocystis pyrifera*) is present in the Strait of Juan de Fuca that extend the boundary to Cape Flattery, but this species is not present in the geographic area of this plan.

sexual, haploid gametophytes. Once sporophytes mature, portions of the blades undergo meiosis to produce distinct patches known as sori that release billions of motile zoospores into the water column (Bartsch et al. 2008; Schiel and Foster 2015). Other species, such as *Macrocystis* and the locally abundant *Alaria marginata*, produce specialized reproductive blades near the base of the plant called sporophylls that produce sori. Dispersal distances for kelp spores are relatively small compared to the larval stages of other marine biota (Gaylord et al. 2002; Suskiewicz 2010). Generally, kelp zoospores fall within several meters of the parent plant. However, zoospore dispersal distance is negatively related to depth, with spores released higher in the water column possibly traveling several kilometers before settling (Gaylord et al. 2002). Additionally, adult plants with pneumatocysts that break free from the benthos, such as *Macrocystis* and *Nereocystis*, can form floating rafts capable of traveling long distances while continuing to produce viable spores (Rothäusler et al. 2009).

Kelp requires solid substrates and will attach readily to both consolidated bedrock and unconsolidated gravel or cobble interspersed in muddy or sandy areas (Dayton 1985). Once attached, the spores germinate after approximately one week into male and female gametophytes that reproduce sexually to produce microscopic germling sporophytes in as little as three weeks. Following this initial recruitment, juvenile sporophytes grow rapidly throughout the entirety of the growing season. In the Salish Sea, macroalgal recruitment and growth occur during the spring and early summer (Druehl and Hsiao 1977; Maxell and Miller 1996).

A.1.2 Kelp Recruitment and Growth

Kelp species exhibit high growth rates, making them competitively dominant in subtidal algal assemblages (Dayton 1985). Persistence of any kelp species is limited by spore availability and the ability to recruit to the available substrate (Reed 1990). Recruitment also depends on species-specific life histories and ambient environmental conditions. Spore production in some perennial species is limited to certain dispersal windows, while annual species produce spores only as long as adult sporophytes are present. If a large disturbance (e.g., marine heatwaves, large storms, booms in grazer populations) results in the loss of most sporophytes before spore dispersal, recruitment may be severely impacted (Wernberg et al. 2010). However, if microscopic life stages are impacted by disturbance, the recruitment dynamic for perennial species can shift from a competition regime between adults and new recruits to one that is wholly dependent on adult sporophytes (Wernberg et al. 2010). In these instances, as is always the case for annual species, any disturbance that removes sporophytes may result in total forest loss.

A.1.3 Microscopic Life Stage Dormancy

For all annual and perennial species with seasonal spore production, there is growing evidence that microscopic forms remain dormant or overwinter until conditions are favorable for reproduction and growth (Carney and Edwards 2006). Evidence points to gametophytes being the most common life stage capable of overwintering, although there is some evidence that spores and germling sporophytes may overwinter as well (Hurd et al. 2014). Controlled laboratory experiments have produced the bulk of evidence for dormancy in microscopic life stages. While these studies are valuable, caution is prudent when generalizing results to *in situ* populations (Schiel and Foster 2015). The abiotic thresholds and biotic stressors for zoospores, gametophytes, and germling sporophytes can differ from those of mature sporophytes and between species. The cryptic nature of microscopic life stages and the logistical difficulties associated with conducting underwater ecological research continue to be the largest hurdles in increasing our understanding of these critical life stages in the field.

A.1.4 Light Availability and Timing of Kelp Recruitment

Kelp sporophytes and gametophytes occupy the photic zone, the area of the nearshore environment where light penetrates to the benthos at a rate where net photosynthesis exceeds respiration (Dayton 1985; Hurd et al. 2014). Generally, one percent of total irradiance is regarded as the boundary of the photic zone (Bertness et al. 2014). However, this boundary depends on the ambient irradiance, which is itself influenced by the timing of low tides, the amount of attenuation or scattering (dependent on suspended sediments and phytoplankton), day length, and the angle of the sun in relation to locale.

Irradiance in Puget Sound shows strong seasonal patterns, increasing ten-fold from approximately 127 µmol/m^2/s in December to 1,348 µmol/m^2/s in July (Knapp n.d.). The timing of the lowest daily tide (Lower Low Water), which occurs during the night in winter and during the day in summer, further influences total benthic light availability. The shift from night to day lower low tides occurs in February and March (late winter). Despite intermediate irradiances (300 to 515 µmol/m^2/s) during late winter, the daytime timing of low tides allows for greater light availability in the nearshore (Knapp n.d.; Druehl and Hsiao 1977). Several studies have observed that this late-winter period of increased light availability coincides with kelp recruitment in the Pacific Northwest (Druehl and Hsiao 1977; Maxell and Miller 1996; Allen 2018).

In a recent *Nereocystis* outplant experiment in the Central Basin conducted by the Puget Sound Restoration Fund (PSRF), Allen (2018) observed that winter transfers of spore, gametophyte, and germlings to the field produced juvenile sporophytes in February and March only. Interestingly, successful recruitment from spore and gametophyte treatments occurred only for treatments outplanted in December, January and February, while only the germling sporophyte treatments successfully produced juveniles in the March treatment. Results on the timing of initial macroalgal recruitment made by Allen (2018) echo similar observations made by Druehl and Hsiao (1977) in Barkley Sound, B.C. and Maxell and Miller (1996) at Titlow Beach in the South Basin of Puget Sound, and point toward the importance of seasonal cues for *Nereocystis* reproduction.

A.1.5 Photosynthetic Performance

Generally speaking, kelp species are light-flexible (shade-tolerant), making them uniquely adapted to the low-light environments created by dense canopies (Clark et al. 2004; Schiel and Foster 2015). Light in kelp forests also varies broadly along spatial and temporal scales because of the constant motion of canopy fronds. Many understory kelp and macroalgal species are specially adapted to capture the “flecks” of sunlight for photosynthesis (Wing et al. 1993).

Photosynthesis occurs at variable rates over a range of irradiances (Hurd et al. 2014). At compensation irradiances, photosynthetic rates match cellular respiration, resulting in increased biomass. Kelp sporophytes generally require 2 to 11 µmol/m^2/s to reach compensation (Hurd et al. 2014). Even though no biomass is lost at compensation irradiances, the ability of any kelp life stage to deal with additional stressors is compromised. In addition, sporophyte sorus production, spore germination, gametophyte reproduction, and germling saprophyte growth may be delayed or impeded at low irradiances (Vadas 1972; Carney and Edwards 2006). For example, germling *Macrocystis* sporophytes delay growth at 2 to 3 µmol/m^2/s (Carney and Edwards 2006). Similarly, Vadas (1972) found that only one percent of *Nereocystis* gametophytes exposed to irradiances of approximately 2 µmol/m^2/s for three weeks attained fertility.

Photosynthetic rates increase with increasing irradiance until maximum photosynthetic rates are attained under saturation irradiances. At this point, any increase in irradiance returns little to no increase in photosynthetic rates. Saturation irradiances for kelp sporophytes fall between 150 to 250 µmol/m^2/s (Hurd et al. 2014). However, there is evidence that saturation levels are significantly lower for microscopic life stages. In laboratory cultures, growth rates of Puget Sound *Nereocystis* gametophytes and germling sporophytes peaked between approximately 15 and 30 µmol/m^2/s at 10 to 15 °C, similar to the critical levels needed to induce germling sporophyte growth in *Macrocystis* (20 to 30 µmol/m^2/s) (Vadas 1972; Carney and Edwards 2006). However, laboratory investigations on the effect of temperature on California *Nereocystis* gametophyte growth rates observed peak gametophyte growth at 77 and 110 µmol/m^2/s in temperatures between13 and 17 °C (Tera Corp. 1982). Whether these discrepancies result from differences in methodology or local adaptations of source populations is unknown, but they highlight the difficulty of accurately describing the reproductive ecology of kelp microscopic life stages from laboratory trials alone. While light is essential for photosynthesis, photoinhibition occurs when high irradiances and UV exposure lead to cellular damage and tissue death. Photoinhibition for kelp generally occurs between 850 and 1000 µmol/m^2/s, with microscopic stages being especially susceptible to UV damage (Swanson and Druehl 2000). However, photo-tolerance, like many traits, is species-specific, with floating canopy species likely adapted to deal with higher ambient irradiances and UV exposure at the water surface.

A.1.6 Temperature Requirements

Individual kelp species have unique optimal temperature ranges that can differ between alternative life stages (Dayton 1985; Harley et al. 2012; Hurd et al. 2014). Temperature optima vary between species and can be difficult to fully describe because populations adapted to local conditions can acclimate to a wide range of temperatures (Lind and Konar 2017; Muth et al. 2019; Hollarsmith et al. 2020).

Cold-water *Laminaria* and *Saccharina* species can survive and reproduce at temperatures from zero to 18 °C but grow optimally in the range of 5 to 15 °C (Bartsch et al. 2008). Similarly, while *Nereocystis* sporophytes can survive at a range of -1.5 °C to 18 °C (Lüning and Freshwater 1988), Maxell and Miller (1996) found that Puget Sound *Nereocystis* stipe and blade growth rates peaked in concert with summer temperatures of 13.5 °C. *Nereocystis* is an annual species, and it is unclear whether temperature or season influenced the peak blade growth rates observed by Maxell and Miller (1996). However, laboratory studies of Puget Sound *Nereocystis* germling sporophytes and gametophytes showed similar optimal temperature ranges between 10 and 15 °C (Vadas 1972). Spore germination rates follow a similar trend, with 60 to 70 percent of Strait of Georgia *Nereocystis* spores germinating at 10 to 15 °C, but only 20 to 30 percent germinating at 17.5 °C (Schiltroth et al. 2018).

Outside of optimal ranges, photosynthetic performance in terms of rate and yield can be augmented by increasing pigment content, reaction centers, and protein complexes, as long as sufficient nutrients are available (Bartsch et al. 2008). Yet, maintaining positive growth in the face of temperature stress may leave adult sporophytes more susceptible to other disturbances (Rothäusler et al. 2009; Wernberg et al. 2010).

A.1.7 Kelp Nutrient Requirements and Regimes in Puget Sound

Seasonal and geographic variations in nutrient availability influence the productivity of kelp species (Dayton 1985; Schiel and Foster 2006). Kelp species, like other autotrophs, are carbon- and nitrogen-limited (Dayton 1985; Hurd et al. 2014). Nutrient availability often tracks negatively with temperature and season (Dayton 1985). While there is not a strong upwelling regime in Puget Sound, dissolved inorganic nitrogen (DIN) concentrations follow a distinct seasonal pattern, peaking during winter months and dropping to near zero in some areas during summer periods of peak algal growth (Khangaonkar et al. 2018). While a majority of DIN is transported into Puget Sound via deeper waters entering from the Strait of Juan de Fuca, anthropogenic nutrient inputs account for 73 percent of surface DIN loads (Khangaonkar et al. 2011; Mohamedali et al. 2011; see ‘Section A.3.6 Human impacts in Puget Sound’ for more discussion on anthropogenic nutrient loading).

Macroscopic kelp sporophytes require suitable nutrients to maintain high growth rates. In California, *Macrocystis* requires a minimum of 1 to 2 µmol inorganic nitrogen/L to support average increases of 4 percent wet weight per day (Schiel and Foster 2015), while nitrate levels of 10 µmol/L are associated with increased *Macrocystis* blade biomass and reductions in blade erosion in New Zealand (Stephens and Hepburn 2016). No information currently exists regarding optimal nutrient ranges for adult *Nereocystis* sporophytes. However, in laboratory studies, juvenile *Nereocystis* sporophyte densities increased significantly when cultivated in 10 µmol nitrate/L as compared to 1 and 5 µmol nitrate/L (Muth et al. 2019). During 2018 field sampling, *Nereocystis* blades at Squaxin Island in SPS were significantly shorter, shredded, and often missing in July when surface DIN concentrations dropped to 0.21 µmol/L—lower than at any other site in the study (Berry et al. 2019; Calloway 2020). There is some evidence that faster-growing annual algae (phytoplankton and ephemeral seaweeds such as *Ulva* spp.) are more susceptible to nutrient limitations than slower-growing perennial species, but this speaks more to their rate of nutrient assimilation than to inherent differences in nutrient requirements (Hurd et al. 2014).

A.1.8 Algal Competition

Seaweeds compete for available space, light, and nutrients (Dayton et al. 1992; Schiel and Foster 2006). Canopy-forming species that recruit to new available substrate first reduce light availability for understory species (Wing et al. 1993; Clark et al. 2004; Hurd et al. 2014). *Nereocystis*, for example, relies on early recruitment and fast growth rates to quickly attain dominance in the canopy, where its floating fronds influence light availability below (Springer et al. 2010; Dobkowski et al. 2019). Reduced light availability from floating canopies directly affects macroalgal and sessile invertebrate understory assemblages, exerting significant control over the structure and composition of kelp forests (Irving and Connell 2002; Clark et al. 2004). Competition between macroalgal species is not limited to the sporophyte stage. Female kelp gametophytes release pheromones to trigger the release and attraction of sperm from the male gametophyte. Species whose gametophytes mature faster may swamp the environment with pheromones thereby increasing recruitment success (Reed 1990). In a field investigation of competition between kelp microscopic life stages, both medium and high densities of *P. californica* gametophytes reduced *Macrocystis* recruitment. *Macrocystis* densities had no effect on *P. californica* recruitment (Reed 1990). While the authors suggest the possibility that such pheromone “chemical warfare” may explain their results, they stress that other confounding variables likely play a role in kelp recruitment success and call for more study on the ecology of kelp microscopic life stages.

A.2 Kelp Distribution and Trends

A.2.1 Global Kelp Trends

Accurately describing long-term trends in global kelp forests is difficult. Kelp generally show a high level of seasonal and inter-annual variability—even more so than is characteristic of other marine ecosystems (e.g., coral reefs) or terrestrial biomes (Krumhansl et al. 2016). Long-term (≥ 20 years) and regional-scale studies provide the best clarity when assessing historical trajectories of kelp forests (Krumhansl et al. 2016; Pfister and Betcher 2017). However, a lack of consistent long-term data sets for subtidal kelp distribution and trends make any global snapshot of kelp reliant on a small and scattered sample of short-term studies.

An analysis by Krumhansl et al. (2016) of long-term (≥ 2 years) kelp monitoring data shows declines in approximately 38 percent of global kelp ecosystems (Krumhansl et al. 2016). Changes in the nearshore environment have led to serious losses of kelp in Australia (Connell et al. 2019), California (Rogers-Bennett and Catton 2019), and Tasmania (Ling et al. 2009; Wernberg et al. 2019). Such localized losses can be severe and difficult to reverse (Wernberg et al. 2019; Filbee-Dexter and Wernberg 2018; Steneck et al. 2002). Despite regional losses, Krumhansl et al. (2016) also found that 35 percent of global kelp forests have shown no change over 50 years. They caution, however, that this could be due to their reliance on sporadic, short-term (< 20 year) studies that lack the power to detect long-term change. The authors also warn that kelp monitoring has declined in frequency and extent over the past five years, making a strong case for increasing long-term kelp monitoring projects.

A.2.2 Puget Sound Kelp Trends

Our current understanding of kelp resources in Puget Sound is largely restricted to canopies formed by bull kelp (and giant kelp elsewhere in Washington waters) since their large surface-floating fronds allow for surveying from boats, aircraft, and satellites. Traditional and local ecological knowledge from Tribes, residents, citizen-science surveys, and analysis of historical data all point to significant declines in the extent and density of bull kelp forests throughout Puget Sound. Little information exists regarding distributions of the other 16 kelp species in Puget Sound as defined by this plan (Mumford 2007).

Collaboration and communication among the different organizations currently monitoring bull kelp forests provide strong evidence for declines in floating canopies. However, no current data or monitoring activities focus on the distributions and trends of understory kelp species.

Local Observations of Loss

Anecdotal observations from residents, Tribes, NGOs, and management agencies consistently describe losses in the number and extent of bull kelp forests in Puget Sound. The Suquamish Tribe witnessed the loss of a large and persistent bull kelp forest near Jefferson Head on the Kitsap Peninsula. PSRF documented the loss of the last remaining Bainbridge Island bull kelp canopy at Tyee Shoal between 2010 and 2015. Similarly, traditional ecological knowledge interviews with Samish elders describe significant losses around the San Juan Islands (Palmer-McGee 2019).

Washington Department of Natural Resources Long-term Monitoring

Annual aerial surveys of the outer coast and Strait of Juan de Fuca by the Washington State Department of Natural Resources (DNR) represent the best long-term monitoring of floating bull kelp and giant kelp canopies for the state. However, these flights incorporate only a small portion of the geographic scope of this plan—the north Quimper Peninsula shoreline (Berry et al. 2005). Within this region, DNR documented significant losses in the canopy area around Protection Island. However, examination of historical records shows that this area exhibited high variability, and observed declines may reflect natural variation (Rigg 1915; Berry et al. 2005). Comparisons of long-term aerial photography of the north Olympic Peninsula to kelp surveys from 1911 to 1912 document declines along shorelines between Dungeness Spit and Port Townsend, in contrast to century-scale stability along the open coast and western Strait of Juan de Fuca (Pfister et al. 2017).

Washington Department of Natural Resources Boat Surveys

DNR compared current and historical bull kelp distribution at sites and identified areas of concern for losses in South Puget Sound, Bainbridge Island, and east San Juan Island, and apparent increases in Elliott Bay (Berry et al. 2014).

Berry et al. (2019) documented major recent declines in all four *Nereocystis* beds monitored in South Puget Sound between 2013 and 2019, a period of extremely warm water conditions. They noted that *Nereocystis* beds in the Tacoma Narrows sub-area were far more abundant and in a healthier condition, with higher numbers of blades and lower severity of physical damage and epiphyte fouling. The authors also observed distinct differences in water column properties known to affect kelp. Nitrogen concentrations were significantly higher in the Tacoma Narrows, with values above 10 µmol/L throughout the year, while they dropped to 1 to5 µmol/L at the innermost site within the basin. Summer water temperatures were consistently higher (Δ1 to 4 °C) in the innermost site, compared to the Tacoma Narrows, and exceeded thresholds known to be deleterious to bull kelp (up to 20 °C). These differences in water column properties could be attributed to the intense tidal mixing that occurs at the Tacoma Narrows.

To establish a complete historical baseline for assessing *Nereocystis* canopy trends, DNR is comparing on-the-water surveys to historical charts and survey data from state and federal agencies. A recently completed analysis of South Puget Sound documented a 62 percent loss in linear extent of *Nereocystis* canopies, with losses significantly more severe in the western and central portions of the basin (Berry et al. 2020; Figure A-1). DNR is currently conducting similar analyses for Central Puget Sound.

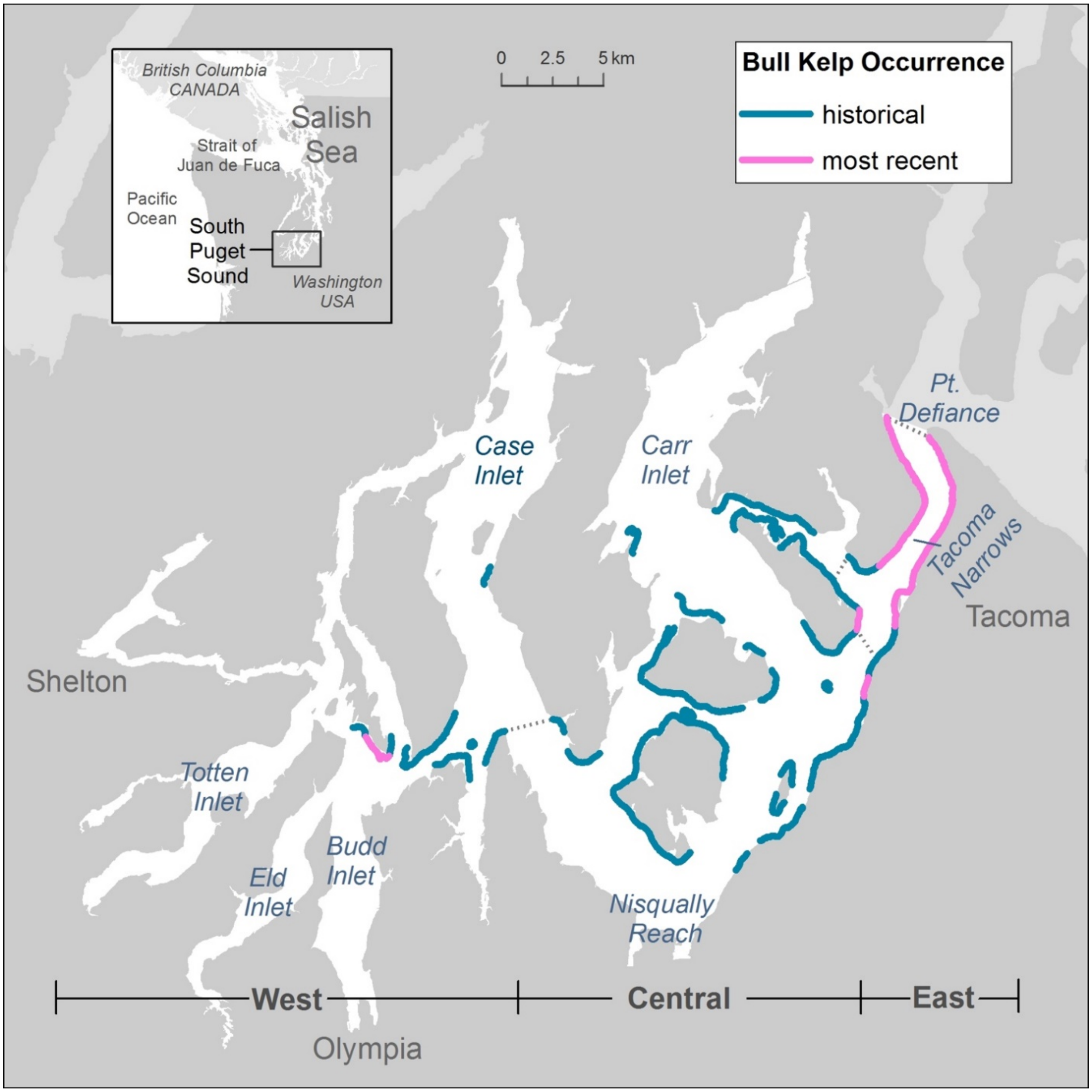

Figure A-1. Historical and recent bull kelp distribution in South Puget Sound. Blue lines delineate shorelines where bull kelp occurred historically but has not been observed recently (all records since 1870s). Pink lines delineate shorelines where bull kelp occurred historically and persisted in most recent surveys (2017-2018).

Northwest Straits Commission Marine Resources Committee Kayak Monitoring

In addition to efforts in the South and Main Basins, the Northwest Straits Commission and seven county marine resources committees (MRCs) conduct citizen-science kayak mapping of bull kelp canopies in the Whidbey Basin, Strait of Juan de Fuca, San Juan archipelago, and North Sound. Citizen-science kayak surveys focus on mapping the surface perimeter of *Nereocystis* canopies and collecting additional data on environmental conditions (e.g., water temperature). Bull kelp beds monitored by the MRCs have been relatively stable from 2015-2019, except for select sites in Snohomish County where the MRC has documented forest losses and declines near Mukilteo and Meadowdale.

A.3 Kelp Stressors

Kelp species thrive in clear, cool waters and their sensitivity to changes in water quality make them potential sentinel species for nearshore environments, with losses often following increases in temperature, nutrient loading, and turbidity (Steneck et al. 2002; Reed et al. 2016; Filbee-Dexter and Wernberg 2018). Development and urbanization are associated with predictable impacts on nearshore environments, including increases in runoff, sediment delivery, and effluent discharges that have the potential to severely affect kelp forests (Heery 2017).

A.3.1 Increased Ocean Temperatures

Global sea surface temperatures (SST) have increased an average of 0.44 °C (0.36 to 0.52 °C) since 1971, while extreme warming events—like the 2014-2016 “blob” that resulted in maximum SST anomalies five to seven degrees Celsius warmer than average in the northeastern Pacific—are likely to increase in severity and frequency (Gentemann et al. 2017; IPCC 2014). No long-term SST data exists for Puget Sound, but records from Race Rocks, Canada (close to Neah Bay, Washington) show a 0.7 °C increase in SST over the past century (Pfister et al. 2017). Warming ocean temperatures and marine heatwaves have, directly and indirectly, led to significant and persistent kelp losses at several locations across the globe (Wernberg et al. 2019; Connell et al. 2019; Feehan et al. 2019; Rogers-Bennett and Catton 2019).

While species-specific temperature tolerances differ, most kelp species in our region are predicted to respond negatively to warming ocean temperatures with lower spore production, germination rates, and recruitment (Muth et al. 2019). Kelp species, especially at the warm edges of their natural distributions, can and have quickly adapted to changes in temperature regimes in the past; but there is a concern that the current rate of SST increase may be too rapid for kelp to adapt naturally (Muth et al. 2019; Feehan et al. 2019; Hollarsmith et al. 2020).

A.3.2 Shifts to Turf-Dominated Assemblages

Turf algae include small filamentous and foliose green and red algae associated with lower community biodiversity and fewer ecosystem services than healthy kelp forests (Connell et al. 2014). Shifts to communities dominated by turf-forming algae are increasing across the globe. They have been recently documented in North Sea *S. latissima* forests (Moy and Christie 2012), southern Australian *E. radiata* stands (Connell and Russell 2010), along developed coasts in the Mediterranean (Benedetti-Cecchi et al. 2001), and the northeastern United States (Feehan et al. 2019). Potentially similar shifts have also been noted in Washington State in proximity to Seattle (Heery 2017).

Shifts to turf-dominated assemblages are a new phenomenon, and researchers are working to pinpoint causes in order to recover lost kelp forests (Filbee-Dexter and Wernberg 2018). Both increased water temperature and anthropogenic nutrient loading seem to lend competitive advantages to turf species, allowing them to quickly monopolize available substrates and block kelp recruitment (Russell et al. 2009; Feehan et al. 2019). In laboratory experiments conducted in

Australia, higher temperatures resulted in significant increases in turf cover on experimental substrates (Falkenberg et al. 2013). Falkenberg et al. (2013) also found that higher temperatures combined with increased CO_2 lead to faster expansion of turf assemblages than would be predicted from either parameter acting alone. Experiments by Falkenberg, Russell, and Connell (2013) show that increased nitrogen availability allows for faster turf expansion, raising concerns about increased anthropogenic nutrient loading in areas experiencing increased coastal development. However, recent research from Rhode Island in the northwest Atlantic documents conversion of kelp habitats to turf assemblages during a period of time when anthropogenic nutrient loads decreased (Feehan et al. 2019). This finding raises serious concerns that increased water temperature alone, more than excess nutrient loading, may explain the recent the rise of turf barrens.

A.3.3 Grazing Pressure

The effects of herbivory on kelp forest systems are well documented in the popular and scientific literature (see Steneck et al. 2002 for a review). While sea otter reintroduction led to some kelp recovery in southeastern Alaska (Estes and Duggins 1995), there is no historical evidence for sea otters in the inland waters of Puget Sound (Everitt et al. 1980). Urchins left unchecked by predators can quickly “clear cut” entire kelp forests, creating barrens devoid of macroalgae and crowded by sickly urchins. Puget Sound hosts three urchin species (*Strongylocentrotus purpuratus*, *S. droebachiensis*, and *Mesocentrotus franciscanus*), but WDFW has not documented extensive urchin barrens during population surveys (personal communication with Henry Carson, WDFW, November 14, 2019). Limited areas characterized by low macroalgae cover and high purple urchin (*S. purpuratus*) densities, however, have been documented along the outer coast of Vancouver Island, the western Strait of Juan de Fuca, and the San Juan Islands (personal communication with Helen Berry and Taylor Frierson, WDFW, November 14, 2019). Purple urchins have been responsible for recent large and persistent kelp losses in northern California, and there is a concern that urchin barrens may be expanding north into Oregon (Flaccus and Chea 2019; Rogers-Bennett and Catton 2019).

While the importance of herbivory from conspicuous macrograzers, like urchins, is critical in understanding kelp forest dynamics (Steneck et al. 2002), smaller mesograzers—such as amphipods, small crustaceans, and small gastropods—may exert a similar negative influence (Duggins et al. 2001; Davenport and Anderson 2007; O’Brien and Scheibling 2016; Pfister and Betcher 2017). Often, pressures from smaller grazers interact synergistically with environmental stress, resulting in greater impacts than expected.

Duggins et al. (2001) investigated the role of current flow on the abundance of the grazing gastropod *Lacuna vincta* and mortality of *Nereocystis* in the San Juan Islands of Washington State. *Nereocystis* mortality was highest in areas that experienced the largest tidal exchanges, despite low *L. vincta* abundances. This mortality was in contrast to low mortality rates found in both low current areas with high *L. vincta* densities and high current areas with low *L. vincta* densities that experienced less dramatic tidal exchanges. This counterintuitive result stems from the interactive effect of current velocity and grazer damage. Duggins et al. (2001) found that even minor damage to *Nereocystis* stipes significantly reduced their breaking strength. During periods of low tidal current velocity, *Lacuna* snails were able to damage *Nereocystsis* stipes enough that high currents during large tidal exchanges resulted in significant sporophyte mortality. Pfister and Betcher (2017) observed similar patterns of mortality associated with wave action and grazer damage to stipes for the upper subtidal species *Pleurophycus gardneri* along the Tatoosh Island coast.

Within Puget Sound, there is concern that grazing from the locally abundant northern kelp crab (*Pugettia producta*) may have similar detrimental effects when acting in concert with above-average water temperatures and high current velocities (Rothäusler et al. 2009). While *P. producta* prefers *Macrocystis* in California, a strong preference for *Nereocystis* has been demonstrated in Puget Sound (Dobkowski 2017; Dobkowski et al. 2019). In subtidal experiments, Dobkowski (2017) found that only *Nereocystis* sporophytes fully protected from *P. producta* grazing increased in wet mass and tissue length. Anecdotal accounts from local recreational boaters in the Bainbridge Island and Olympia areas often attribute kelp losses to increases in *P. producta* abundance (personal observation). There is no current information regarding the large-scale impacts of locally abundant herbivores on Puget Sound kelp distribution and persistence.

It is important to note that grazing, when checked, acts as an influential intermediate and ongoing disturbance that may promote increased macroalgal diversity. In Alaskan *Saccharina groenlandica* and *Nereocystis* forests, Duggins (1980) found that kelp diversity decreased over the long term following the experimental removal of urchins. In the absence of regular disturbance, the large perennial *S. groenlandica* quickly monopolized the benthos, excluding most other macroalgae, including *Nereocystis*.

A.3.4 Sediment Effects on Microscopic Life stages and Turbidity

Changes in sediment transport, deposition rates, and particle size can have significant impacts on kelp recruitment and persistence. While sediment does not generally induce mortality in large sporophytes, increases in water turbidity can starve kelp of light and cause significant mortality to kelp spores, gametophytes, and germling sporophytes (Deiman et al. 2012; Geange et al. 2014; Watanabe et al. 2016).

Mortality of microscopic life stages results from suffocation by suspended or smothering sediments or through the prevention of attachment to substrates by settled sediment. In laboratory experiments on the effect of suspended and settled sediments on *Nereocystis* and dragon kelp (*Eualaria fistulosa*, closely related to *Alaria marginata* found in Puget Sound), suspended sediment loads of 420 mg/L resulted in only six percent average spore attachment, while settled sediment reduced spore attachment by nearly 99 percent (Deiman et al. 2012). A similar study on *Macrocystis* and *Undaria pinatifidia* (an introduced cousin of *A. marginata*) spore germination suggests that sediment loads greater than 100 mg/L may be enough to severely impact gametophyte densities (Geange et al. 2014). Studies on the Japanese canopy species *Eisenia* *bicyclis* show that loads as low as 30 mg/L led to 100 percent mortality in laboratory-grown gametophytes (Arakawa 2005).

Whether sediment is an issue for Puget Sound kelp is currently unknown. Observed suspended sediment concentrations (SSC) for South Puget Sound rarely exceed 2 mg/L (Berry et al. 2019). However, wave action and tidal currents complicate efforts to measure *in situ* benthic sediment accumulation and SSC (Storlazzi et al. 2011). Furthermore, sediment-associated pollutants from urban and agricultural runoff may lead to higher mortality, even when accumulation rates and SSC are below known mortality thresholds. Unfortunately, little data exists on adult sporophyte or microscopic life stage response to common runoff-associated pollutants.

Increased sediment transport to the nearshore can also negatively affect kelp populations by increasing turbidity. Kelp beds at the mouth of the Elwha River completely disappeared for several years following the removal of two large dams (Rubin et al. 2017; Glover et al. 2019). Total sediment flux during the six months of April through September in the three years (2012-2014) following dam removal was more than 0.65 Mt, 2.4 Mt, and 0.1 Mt, respectively. Kelp and other macroalgae were abundant at all study sites before dam removal but declined dramatically in the first two years afterward (Rubin et al. 2017). Kelp and macroalgae cover remained sparse during the spring of 2014 but recovered significantly following a surprise recruitment event in late summer. While such large sediment loads can lead to significant mortality for microscopic life stages (Deiman et al. 2012; Watanabe et al. 2016), Rubin et al. (2017) attributed the late-season recruitment event to the low sediment fluxes recorded in late summer of 2014 (<500 tonnes/day), which resulted in greater light availability for dormant microscopic life stages. Subsequent analysis by Glover et al. (2019) identified the primary driver of light attenuation to be suspended sediment, with measured chlorophyll-a and colored dissolved organic matter (CDOM) concentrations contributing < 15 percent to observed attenuation values. Modeling showed that total daily benthic light availability was below 1 to 2 µmol/m^2/day in 2013 and seasonally in 2012 and 2014, supporting the hypothesis that reduced light availability caused the mortality event. Light availability increased in 2016 and 2017 as the annual sediment load decreased in tandem with the reestablishment of the macroalgal community.

A.3.5 Invasive Seaweed: *Sargassum muticum* and *Undaria pinnatifida*

There is concern that the invasive *Sargassum muticum* may disrupt native algal succession in Puget Sound by altering light availability (Britton-Simmons 2004). In experiments conducted in the San Juan Islands, Britton-Simmons (2004) documented a 75 percent reduction in the abundance of native prostrate kelp species in shallow waters. The authors attributed these declines to *S. muticum*’s early growth, which blocked light for native species that recruit slightly later. The authors also demonstrated in feeding trials that *Sargassum* is less palatable to local invertebrates. Considering the significant contribution of kelp-derived biomass to nearshore ecosystems (von Biela et al. 2016), large-scale shifts to *Sargassum*-dominated habitat may potentially have negative effects that cascade up Puget Sound food webs. Additionally, *Sargassum* is more temperature tolerant than native kelp species, and may persist and expand in tandem with increasing SST.

Undaria pinnatifida has been encountered as far north as San Francisco along the California coast (Zabin et al. 2009), and there is concern over its potential presence in Washington State waters and Puget Sound. There is no evidence for *Undaria* in Puget Sound, but in the absence of comprehensive understory kelp surveys, its presence is currently unknown. While *Undaria,* like *Sargassum*, is a common invasive species throughout the Pacific, there is no consensus regarding its impacts on native kelp assemblages (Casas et al. 2004; South et al. 2017).

A.3.6 Human Impacts in Puget Sound

As of 2017, the Washington State population has increased over 300 percent since 2010, with considerable growth in coastal areas ("Population Trends, Washington State," n.d.). From 2000 to 2017, the Puget Sound region saw a 26 percent increase in new housing units (Washington Department of Commerce 2017). Most of this growth occurred in and around the cities of Seattle, Bellevue, Everett, and Tacoma, but above average rural and urban development occurred in Whatcom, Skagit, Kitsap, and Thurston counties as well.

Urbanization and development are associated with predictable changes to the nearshore environment. Nutrient pollution from increased wastewater treatment plant (WWTP) effluent, increased water temperatures, and decreased salinity and increased sediment and contaminant delivery caused byrunoff all interact to create different conditions in urban nearshore environments (Howarth et al. 2002; Heery 2017). Of particular concern for nearshore kelp beds are increased point source WWTP discharge and non-point sources of pollution from runoff.

Modeling from 2011 estimates for DIN loading from all human point and non-point sources accounted for 73 percent of total DIN loads (Mohamedali et al. 2011). Annual average WWTP DIN loads were 1.4 times greater than river inputs, but were 4.3 times higher in summer months, a time when excess anthropogenic nutrients inputs can have greater impacts to Puget Sound dissolved oxygen and phytoplankton blooms (Mohamedali et al. 2011). While large-scale eutrophication has not been a concern in Puget Sound, the Washington State Department of Ecology (DOE) has identified excessive levels of nutrients from human sources as a major threat to water quality in Puget Sound (DOE 2019). Additionally, DOE has listed many water bodies with degraded water quality on the federally mandated 303d list. Studies from Australia and Europe documented increases in turf algae and decreases to kelp canopies even in non-eutrophic waters (Airoldi and Beck 2007; Falkenberg et al. 2013). Potentially similar shifts have been documented in proximity to urban areas in the Main Basin of Puget Sound (Heery 2017).

Toxic Contaminants

While there is serious concern about the toxic effects of common pollutants on Puget Sound kelp populations, there is little available information. Eklund and Kautsky (2003) found 82 studies on macroalgae toxicity published from 1959 to 2003, with relatively few substances being tested on more than one species. Out of 65 species included in the surveyed literature only 12 were

Laminariales species and only *S. latissima* and *Macrocystis* had more than 2 published toxicity studies—10 and 4 respectively (Eklund and Kautsky 2003).

Copper toxicity on kelp is fairly well understood and accounted for 41 percent of the studies compiled by Eklund and Kautsky (2003). Studies showed exposure often reduced spore release, and inhibited or delayed gametophyte germination and reproduction, and juvenile sporophyte growth (Eklund and Kautsky 2003; Leal et al. 2018). In addition to contaminants from point and non-point sources, there is particular concern in the Salish Sea over impacts of oil spills (Niu et al 2016). Unfortunately, only one study to date investigates the effects of petroleum exposure on Puget Sound kelp species. Laboratory studies conducted after the 1991 “Tenyo Maru” oil spill in the western Strait of Juan de Fuca found that exposure to diesel and crude oil bleached *Nereocystis* blades and stipes, severely impacting photosynthetic performance (Antrim et al. 1995). The authors note that petroleum products, which tend to float, may have a greater impact on floating species than understory populations. Regardless, more research is needed to fully understand the impacts large petroleum spills and exposure to common contaminants may have on kelp populations.

Landscape-Scale Changes

Human activity has fundamentally altered the shores and catchments of Puget Sound. Coastal development has altered the structure and function of 99.8 percent of Puget Sound shorelines, while broad-scale land use changes in the catchments that empty into Puget Sound have impounded 37 percent of the total drainage area and converted or harvested roughly 50 percent of all lowland forests and wetlands (Pearson et al. 2018). Together, these changes significantly alter terrestrial-nearshore linkages by negatively impacting the ability of the landscape to retain water, sediments, and nutrients.

Changes to catchment-scale processes may affect kelp, as Puget Sound has considerable freshwater inputs from the Skagit, Stillaguamish, Snohomish, Duwamish, Puyallup, Nisqually, and Deschutes rivers (Ebbesmeyer et al. 1988). Of particular concern is the potential for land use changes to increase sediment delivery to estuarine environments. For example, 1,080 landslides occurred in the Stillaguamish watershed between the 1940s and 1990s (Perkins and Collins 1997). While such landslides are a natural part of watershed disturbance regimes, subsequent analysis revealed that road construction and clearcutting practices were responsible for 75 percent of these slides.

Increased sediment loads can have significant impacts on overwintering microscopic forms of kelp. However, the implications depend on the timing of landslide-related sediment deposition, as well as the level of exposure at a given kelp bed (Spurkland and Iken 2011). Winter sediment pulses could potentially smother overwintering kelp gametophytes and sporophytes, while spring sediment pulses could significantly delay recruitment due to increased turbidity. Whether changes in estuarine sediment dynamics affect nearby kelp beds is a concern in Alaska, where increased glacial melt due to climate change heavily influences river sediment loads. While Puget Sound is less affected by glacial melt, residential, commercial, and industrial development increases runoff and hardens shorelines, significantly influencing nearshore processes.

Shoreline armoring dominates nearshore development, accounting for 74 percent of artificial shorelines (Pearson et al. 2018). A long-term study of sediment grain-size along armored and unarmored beaches showed clear relationships between beach sediments and armoring, but no clear connections between lower-intertidal sediments and armoring (Dethier et al. 2016). While no causal link has been identified, it is generally recognized that armoring simplifies shorelines and interferes with natural processes that maintain shoreform structures (Pearson et al. 2018). Such interference may potentially alter substrate availability for kelp recruitment in Puget Sound, but more research is needed to understand these links.

Historic Impacts of Fisheries

Increased commercial and recreational fishery landings in the 1970s and 1980s significantly altered Puget Sound's trophic structure (Harvey et al. 2012). The abundance of Puget Sound rockfishes as a group has declined by about 70 percent over the last 40 years, and overfishing is considered a primary reason for this decline (Williams et al. 2010). Fishing pressure also historically focused on finfish, urchin, sea cucumber, pinto abalone, and geoduck for export markets. The diversity of species targeted for commercial and recreational harvest encompasses nearly the entire range of Puget Sound trophic levels, from suspension-filter feeders to apex predators, suggesting the possibility for severe impacts on trophic functionality (Steneck et al. 2004). This trend of "fishing down the food web" is not unique to Puget Sound, and can negatively affect ecosystem resilience by removing entire functional groups from trophic systems.

Fishery landings for most Puget Sound finfish species peaked and plateaued in the 1970s and 1980s before significantly declining (Essington et al. 2018). Assessments following observed declines led to the closure of Puget Sound commercial cod (*G. maccrocephalus*) and hake (*Merluccius productus*) fisheries, as well as the closure of the recreational walleye pollock (*G. chalcogrammus*) fishery (Gustafson et al. 2000). Of eight salmonids found in the Puget Sound, four—Chinook salmon (*O. tshawytscha*), chum salmon (*O. keta*), bull trout (*Salvelinus confluentus*) and steelhead (*O. mykiss*)—are listed as threatened under the ESA, and two populations of Puget Sound rockfish—yelloweye (*S. ruberrimus*) and Boccaccio (*S. paucispinis*)—were recently listed (64 Fed. Reg. 14308, March 24, 1999; 64 Fed. Reg. 14508, March 25, 1999; 72 Fed. Reg. 26722, May 11, 2007; 75 Fed. Reg. 63898, October 18 2010; National Marine Fisheries Service 2017). Since the adult finfish stocks occupy intermediate to top trophic levels, they play an essential role in maintaining healthy linkages within Puget Sound's trophic system (Steneck et al. 2004; Davenport and Anderson 2007). For instance, various rockfish species feed on kelp crab and other invertebrates that eat kelp (Washington et al. 1978). Grazer abundances are likely to increase in the absence of top-down controls, possibly causing serious harm to Puget Sound kelp resources. Invertebrate fisheries—specifically for urchin and sea cucumber—are still open for harvest, but the impacts of these activities on kelp populations are unknown.

A.4 Kelp as Foundational Species

Like eelgrass, kelp is a critical foundation species that structures broader community assemblages and promotes increased biodiversity by increasing food web complexity and providing critical habitat (Caro 2010; Altieri and van de Koppel 2014). All marine vegetation form living habitats, but kelp provides 25 times more habitat biomass per unit area than seagrass (Teagle et al. 2017). This abundance of biomass creates large volumes of high-quality habitat, much in the same way that high-rise apartment complexes allow for increased population densities in urban areas. The food and shelter provided by kelp cascades up the food chain, ultimately helping to support high-level predators such as birds and marine mammals (von Biela et al. 2016).

A.4.1 Kelp Forests as Critical Finfish Habitat

On large scales, kelp distribution explains variation in fish communities (Pérez-Matus and Shima 2010, 2010). Initial larval settlement often occurs at the first patch of suitable kelp habitat encountered, regardless of quality, as a refuge from predation (Munsch et al. 2016). For many fish species, juvenile survival is linked to growth rate (Duffy et al. 2010; O’Brien et al. 2018). The combination of high-quality refuge and ample foraging opportunities characteristic of kelp forests may help ameliorate stress responses associated with non-consumptive predator effects, further enhancing juvenile survival (Donelan et al. 2017).

In Puget Sound, kelp forests are critical habitat for juvenile rockfish (*Sebastes* spp.), forage fish (including Pacific herring and surf smelt), Pacific cod (*Gadus microcephalus*), and out-migrating juvenile and returning adult salmon (*Oncorhynchus* spp.) (Doty et al. 1995; Shaffer 2000; Duffy et al. 2010).

Increased Invertebrate Abundances

At the individual level, a single kelp provides two to three distinct microhabitats for small invertebrates: the holdfast, the stipe, and the lamina (blade) (Teagle et al. 2017). While holdfast morphology, size, and volume of interstitial space vary widely between species, these structures can host approximately 30 to 70 unique species, with assemblages dominated by amphipods, copepods, and polychaetes (Christie et al. 2009; Teagle et al. 2017). Stipes and blades, on average, harbor fewer distinct taxa but support higher abundances of associated fauna. In California, Miller et al. (2018) observed abundances of shrimp and amphipods exceeding 8,000 individuals per kilogram of giant kelp frond wet weight. *Macrocystis* forests often contain 2.5 to five kg/m^2 of fronds, translating to shrimp and amphipod densities of between 20,000 and 40,000 per square meter. Similarly, structure-associated harpacticoid copepods and decapods (important forage fish and juvenile salmonid prey species) were significantly more abundant inside of Strait of Juan de Fuca kelp forests than in adjacent open water (Shaffer et al. 2020). As a result, invertebrate abundances in kelp forests can be five times greater than in seagrass and other (non-kelp) seaweed habitats and include important fish prey including copepods, amphipods, and shrimp and crab larvae (Penttila 2007; Christie et al. 2009; Duffy et al. 2010; Shaffer et al. 2020).

Forage Fish

Kelp forests, like eelgrass, provide important spawning and rearing habitats for forage fish (Johnson n.d.; Essington et al. 2018). In Puget Sound, forage fish rely on shallow nearshore environments and kelp forests for spawning and foraging success (Shaffer et al. 2020; Shaffer 2000). Large blades provide prey-dense refuges where mid-trophic species like forage fish can feed in relative safety (O'Brien et al. 2018). Pacific herring (*Clupea pallasii*) spawn directly onto submerged aquatic vegetation and, along with surf smelt (*H. pretiosus*) are more abundant in Salish Sea kelp forests than adjacent open water habitats (Shaffer et al. 2020). In addition, sand lance (*Ammodytes hexapterus*) and surf smelt will preferentially aggregate along the edges of kelp beds close to the shore to balance foraging opportunities with refuge from predation (Shaffer 2004). This is not a surprise, as forage fish are generally planktivorous, and kelp beds harbor greater diversity and abundance of marine invertebrates than kelp-free areas (Shaffer et al. 2020; Siddon et al. 2008; Christie et al. 2009).

Rockfish

Juvenile rockfish, like forage fish, preferentially recruit to floating kelp canopies to take advantage of copepods, amphipods, and other abundant zooplankton (Singer 1985; Love et al. 1991). During 1995 surveys of nearshore vegetated habitats, Puget Sound young-of-year (YOY) rockfish were found in 56 percent of all *Nereocystis* stands surveyed, but only 19 percent of eelgrass beds and 15 percent of seaweed forests without a floating canopy (Doty et al. 1995). As juvenile rockfish grow, they seek out deeper water and larger prey items, moving from the floating canopy to kelp understories before maturing and moving to deeper water (Love et al. 1991). Exported kelp wrack and detritus transported to deep-water habitats are an important food subsidy for deep-water invertebrates and likely help indirectly support deep-water groundfish and finfish populations (Britton-Simmons et al. 2012; Krumhansl and Scheibling 2012; Filbee-Dexter and Scheibling 2016). Recent WDFW underwater video surveys observed adult rockfish aggregating in proximity to kelp mats that had drifted to waters deeper than the photic zone where kelp originates, suggesting exported kelp biomass may be important for adult rockfish populations.

Salmon

Together with eelgrass meadows and saltmarshes, kelp forests are a critical part of juvenile salmon outmigration corridors. Juvenile salmon exhibit similar strategies to YOY rockfish, showing a preference for shallow nearshore environments and overwater structures, including kelp canopies (Shaffer 2004; Toft et al. 2007; Shaffer et al. 2020). Stable isotope analysis of native Salish Sea salmon species shows that nearshore kelp food webs remain important for Chinook and coho salmon throughout adulthood (Johnson and Schindler 2009). As a result, recreational fishers and others often search the edges of bull kelp forests when looking for Chinook salmon (personal communication with Dan Tonnes, NOAA, July 17, 2019; WDFW 2020). Researchers in Alaska and Washington have also documented preferential associations between juvenile salmon and submerged and floating kelp forests (Johnson n.d.; Shaffer 2004).

A.4.2 Kelp in the Food Web

Primary production in kelp forests is greater per unit area than in tropical rainforests (Krumhansl et al. 2016), and, in Washington State waters, kelp biomass production is up to six times that of phytoplankton per unit volume (Pfister et al. 2019). This high productivity helps support complex food webs both inside kelp forests and in neighboring deep-water and shoreline habitats (Duggins et al. 1989; Krumhansl et al. 2014). Deep-sea mats of kelp detritus and heaps of kelp wrack on sandy and rocky coasts act as temporary oases, supporting booms in invertebrate populations that, in turn, help support adjacent food webs (Krumhansl and Scheibling 2012).

It is possible to trace kelp-derived carbon through food webs using carbon (∂^{13}C) isotopes because kelp detritus generally has a higher carbon isotopic value than associated phytoplankton (Fredriksen 2003; Miller and Page 2012; von Biela et al. 2016). As shown in Table A-2, such analyses consistently demonstrate the significant role that kelp-derived carbon plays in subsidizing kelp forest food webs (Table A-2). Small invertebrate grazers in Norwegian kelp beds had carbon isotopic signatures very similar to those of associated kelp species, with kelp-derived carbon consistently accounting for 50 percent to nearly 100 percent of the biomass in some gastropod species (Fredriksen 2003). In Alaskan kelp beds, kelp-derived carbon constitutes 57 percent of the muscle biomass in black rockfish *(Sebastes melanops)* and kelp greenling *(Hexagrammos decagrammus)* (von Biela et al. 2016). While these numbers are impressive, a recent review suggests the contribution of kelp-derived carbon may be overstated due to the reliance on offshore phytoplankton for comparative carbon values (Miller and Page 2012). However, the authors noted that this should not be taken to mean that the contribution of kelp-derived carbon to nearshore food webs is inconsequential, simply that more research is required to accurately assess contributions.

Table A-2. Kelp-derived carbon in common Puget Sound fauna, modified from von Biela et al. 2016.

Common Name	Species	Location	Kelp Carbon Contribution
Herring	*Clupea pallasi* (juv.)	Vancouver Island, BC, Canada	35–45 percent
Cod*	*Gadus morhua* (open sea) *	Finnøy, Norway	40 percent
	Gadus morhua (kelp forest) *	Finnøy, Norway	59 percent
Kelp Greenling	*Hexagrammos decagrammus*	northeast Pacific Ocean	39–99 percent
Rock Greenling	*Hexagrammos lagocephalus*	Aleutian Islands, AK, USA	15–75 percent
Kelp Rockfish	*Sebastes atrovirens*	Santa Barbara, CA, USA	35–45 percent
Copper Rockfish	*Sebastes caurinus*	Vancouver Island, BC, Canada	55–65 percent
Black Rockfish	*Sebastes melanops*	Vancouver Island, BC, Canada	50–60 percent
	Sebastes melanops (juv.)	Vancouver Island, BC, Canada	35–45 percent
	Sebastes melanops	northeast Pacific Ocean	35–81 percent
Blue Rockfish	*Sebastes mystinus*	Santa Barbara, CA, USA	10–25 percent
Cormorant	*Phalacrocorax pelagicus*	Aleutian Islands, AK, USA	30–70 percent
Harp Seal*	*Phoca groenlandica* *	Baffin Island, Canada	20 percent
Ringed Seal*	*Phoca hispidia* *	Baffin Island, Canada	9 percent

*Proxies for similar Puget Sound species, all other listings represent species present in Puget Sound.

A.5 Ecosystem Engineering

Kelp forests also create conditions for increased community diversity by altering physical conditions within forests (Altieri and van de Koppel 2014; Miller et al. 2018). The structural complexity, size, and area that large kelp forests occupy influences the aquatic environment by attenuating water and particle flow within and around beds (Eckman et al. 1989; Duggins et al. 1990; Gaylord et al. 2007). This dampening of water motion increases the residence time of nutrients and particles within *Macrocystis* forests, allowing associated seaweeds and filter-feeders to take full advantage of nutrients and food that would otherwise be swept quickly over the reef. Beneath canopies, understory kelps simultaneously retain particulate matter, block sediment accumulation on the benthos (Eckman et al. 1989; Duggins et al. 1990), and help sweep sediment from the benthos, maintaining access to hard substrates for sessile invertebrate larvae and kelp spores (Kennelly 1989; Arkema et al. 2009).

Furthermore, rapid growth makes kelp species some of the most productive autotrophs in the world, with primary productivity exceeding that of cultivated agricultural fields and tropical rain forests per unit area (Krumhansl et al. 2016). The result is an estimated primary productivity above 1,200 g/cm^2/year (Christie et al. 2009). Such an efficient transformation of nutrients and carbon into new biomass may have important implications for the global carbon budget, ocean acidification, and nutrient pollution,

A.5.1 Kelp Carbon Sequestration

Recent estimations by Krause-Jensen and Duarte (2016) suggest that deep-sea deposition and burial of seaweed biomass in nearshore sediments effectively sequesters 173 TgC per year. This estimate exceeds that of carbon sequestration from salt marshes, mangrove forests, and seagrass beds combined. While impressive, these are rough estimates based on data from the available literature, and the authors acknowledge the need for a more detailed analysis of the role of macroalgae in long-term global carbon sequestration. Furthermore, kelp carbon is extremely labile and quickly respired back into the environment, meaning long-term kelp carbon sequestration relies heavily on deep-water deposition and burial.

There is also a growing interest in using kelp aquaculture as one part of broader climate mitigation portfolios, specifically to offset carbon emissions from global aquaculture and regional agriculture sectors (Froehlich et al. 2019). However, kelp aquaculture carbon mitigation requires the development of suitable technologies to transport large volumes of biomass to deep ocean areas where the carbon is most likely to remain sequestered for significant amounts of time—technology that is still in development. Froehlich et al. (2019) estimate that 14 to 25 percent of current global seaweed production would be required to offset total emissions from the global aquaculture industry, suggesting that co-culture of seaweed with other commercial aquaculture species could present a viable way for sustainable, zero-emissions growth of the global aquaculture sector. While seaweed aquaculture may be impractical for offsetting global agricultural emissions, it may be a viable way for regional agricultural sectors to neutralize carbon emissions. California's agricultural sector, for example, could be carbon neutral by utilizing 3.8 percent of the West Coast Exclusive Economic Zones (EEZs) or 0.065 percent of total suitable global waters (Froehlich et al. 2019) for seaweed aquaculture.

A.5.2 Ocean Acidification Amelioration

Carbon uptake and oxygen respiration during photosynthesis may allow kelp species to ameliorate ocean acidification (OA) conditions (Nielsen et al. 2018). However, kelp forests do not export associated increases in water pH levels, and changes in pH are marked by significant depth and diel variation. During daytime photosynthesis, kelp—like other autotrophs—draw up carbon and release oxygen before releasing carbon back into the water during nighttime respiration. Measurement of pH within kelp forests reflect this diel cycle, increasing during the day and decreasing to ambient levels during the night. Despite this diel cycle, the pH in kelp forests along the Strait of Juan de Fuca was, on average, 0.08 points higher than adjacent waters with total diel variation ranging from 0.17 to 0.35 pH units (Pfister et al. 2019). While increases in pH and aragonite saturation are largely restricted to daylight hours, there is evidence that calcifying organisms may time growth to take advantage of this daily amelioration of OA conditions (Wahl et al. 2018). In addition, filter-feeding organisms grow more quickly in kelp forests due to the entrainment of particulate matter characteristic of these habitats (Duggins et al. 1989). This combination of temporary increases in pH and aragonite saturation and increases in food availability makes kelp forests potential "phytorefugia" from OA conditions. While kelp may provide limited local benefits for calcifying organisms, kelp forests are by no means a "silver bullet" for OA conditions.

A.5.3 Nutrient Bioextraction

Nutrient bio-extraction refers specifically to the use of kelp to extract excess nutrients from eutrophic coastal waters (Kim et al. 2017). A handful of studies have focused on the potential for commercial kelp aquaculture to reverse eutrophic conditions, and results from China and the eastern United States show promise (Fei 2004; Kim et al. 2015). Using the nitrogen content of cultivated seaweed tissue as a proxy, Fei et al. (2004) estimated that seaweed aquaculture has the potential to remove 6,600 mg/m^3 of nitrogen from the first two meters of surface waters in a one hectare farm (or roughly up to 528,000 mg/m^2). This number far exceeds the level (400 mg/m^3) used as a benchmark for nitrogen eutrophication. Similarly, Kim et al. (2015) determined that sugar kelp cultivation could potentially remove up to 274,000 mg/m^2 of nitrogen per year from waters in New York's Long Island Sound.

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