NWSC/NOAA Kelp Conservation and Recovery Plan – Literature Review Draft

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INTRODUCTION

Kelp—the largest of all seaweeds—provides an array of valuable ecosystem goods and services to nearshore environments and communities. These underwater forests act as foundations for diverse and productive nearshore ecosystems, subsidizing food webs and providing critical habitat for a wide array of marine fauna (Christie, H. et al. 2009; Steneck, R. S. et al. 2002; Biela, V. R. von et al. 2016). Historic, anecdotal, and monitoring data offer strong evidence for regional kelp losses around the world, but patchy and inconsistent data make describing trends difficult. Management is further complicated by general knowledge gaps pertaining to reproductive ecology and response to cumulative, interacting stressors for kelp ecosystems.

Here in the Puget Sound region, there is growing concern that the canopy-forming bull kelp, *Nereocystis luetkeana* (hereafter *Nereocystis*), may be experiencing significant declines. However, our understanding of kelp biology and physiology historically comes from outer-coast upwelling systems whose oceanographic processes differ from those found in the Puget Sound (Ebbesmeyer, C. C. et al. 1988; Schiel, D. R. & M. S. Foster 2015). While large-scale environmental conditions do explain long-term trends in kelp canopy cover and abundance, local oceanographic processes play a significant role in determining annual variation and persistence (Krumhansl, K. A. et al. 2016; Pfister, C. A. et al. 2017). Thus, Puget Sound kelp response to various stresses and pressures can be inferred to some extent from the available literature, but long-term recovery must address significant gaps in our knowledge about where, how, and why kelp is distributed in Puget Sound and how site-specific differences in local conditions constrain or promote kelp persistence and connectivity.

This recovery plan represents a first step toward contextualizing the trends of the 24 species of kelp found in Puget Sound within the current available literature on kelp biology, ecology, and trends. Furthermore, it is helpful to situate kelp recovery efforts within a framework that recognizes human activity's role in shaping and altering ecosystems. To this end, this plan adopts the European Environmental Agency's Driving Forces, Pressures, State, Impact, Response (DPSIR) framework in order

to plan responses aimed at increasing the resilience, persistence, and abundance of Puget Sound kelp beds (Kristensen, P. 2004).

The plan first builds a general foundation regarding the physical processes of Puget Sound, the general biology and ecology of kelp species, and the habitats they create. Next, we discuss kelp trends throughout the world and point out several broad-scale trajectories that declining kelp beds historically follow. This discussion focuses on the impacts of interactions between local environmental and biotic conditions in determining the fate of kelp forests in a rapidly changing nearshore world. The review will then present a more local perspective summarizing kelp trends in Puget Sound and discussing how local drivers and stressors impact nearshore kelp beds. Specific emphasis will be given to the topic of extent and in what manner do federally listed species of Puget Sound finfish rely on kelp habitats. Finally, the recovery plan concludes by discussing possible responses to data gaps for Puget Sound kelp ecosystems and recommendations for kelp protection and recovery. Specifically, we will show that current gaps in kelp response to Puget Sound specific pressures in combination with a lack of data regarding kelp distribution and abundance currently impede the ability to develop significant and sustainable recovery actions.

PUGET SOUND: PLACE, PROCESSES

Puget Sound is an estuarine system of glacially scoured channels, or fjords, made up of four basins connected by shallow, constricted passages. Defining and subdividing basins is an interpretive task, but for the purposes of this document the four basins include the San Juan archipelago, Hood Canal, Main Basin (composed of Admiralty Inlet, Central Basin, and Whidbey Basin) and South Basin. The working seaward boundary adopted by this plan is the Victoria Sill—a line connecting Green Point (48 d 07.254 m, -123d 17.268m) on the Olympic Peninsula, Washington and Trial Island/Gonzales Point (48d 24.674m, -123d 17.65m) on Vancouver Island, Canada (Tolimieri, N. et al. 2016). A fifth basin located in the Georgia Strait of British Columbia is included to illustrate the full extent of what this plan will refer to

as the Salish Sea. The Strait of Juan de Fuca is excluded from this working definition of Puget Sound and the Salish Sea because of its oceanographic similarity to outer-coast systems.

Each basin is separated by a shallow constriction (Ebbesmeyer, C. C. et al. 1988). Admiralty Inlet not only functions as the primary constriction separating the San Juan Basin and Main Basin, but also as the secondary constriction separating the Hood Canal and Main Basin. Admiralty Inlet also serves as the boundary for subdividing the Main Basin further into the Central Basin –encompassing the deepest waters found in the Puget Sound – and Whidbey Basin, which includes waters between Whidbey Island and the mainland. The Tacoma Narrows forms a tertiary constriction between the Main and South Basins. Finally, the South Basin is subdivided into three sub-basins by the Nisqually Sill and Dana Passage.

Waters of the San Juan, Main, and South Basins of Puget Sound are generally well circulated as a result of turbulent mixing of surface and deeper waters at constriction points (usually the shallow sills) during large tidal fluxes. However, the waters of Hood Canal and Whidbey Basin are more stratified because of slower circulation and considerable freshwater inputs (Williams, G.D., R.M. Thom, J.E. Starkes, J.S. Brennan, J. P. Houghton, D. Woodruff, et al. 2001). A majority of water mixing occurs at constriction points with approximately 50 percent of all water being recycled at a given constriction (Ebbesmeyer, C. C. et al. 1988). This recycling results in residence times of 3 to 6 months for dissolved materials. Dominant surface flows are seaward up to a depth of approximately 50 meters at which point they shift to predominantly landward flows.

Puget Sound is characterized by large tidal fluxes that produce strong currents. Puget Sound tides are mixed-semidiurnal and characterized by two unequal low and two unequal high tides in a given lunar day (Williams, G.D., R.M. Thom, J.E. Starkes, J.S. Brennan, J. P. Houghton, D. Woodruff, et al. 2001). Tidal range varies from 3 to 5 meters and is larger in the interior reaches of the South Basin than in the more open northern basins. These large tidal exchanges result in significant tidal currents often in excess of 1 meter/second (m/s) in many areas and approaching 2 to 3 m/s in the shallow constrictions between basins (Mofjeld, H. O. & L H Larsen 1984).

OVERVIEW OF KELP 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, P. K. 1985). Worldwide, the Laminariales consist of approximately 147 different species, including *Laminaria* spp., *Saccharina* spp., and iconic canopy species such as *Nereocystis* and *Macrocystis pyrifera* (hereafter *Macrocystis*) (Druehl, L. D. & B. E. Clarkston 2016; Teagle, H. et al. 2017). Approximately 24 species of kelp occur in Puget Sound, but species are unequally distributed between basins (Gabrielson, P. W. 2012). Kelp can be annual or perennial depending on the species, but even *Pterygophora californica,* one of the longest-lived species, only persists 15 years at most (Schiel, D. R. & M. S. Foster 2006).

Kelp form structurally diverse habitats composed of multiple species and stories that rise several meters above the benthos and can extend up to 10 to 30 meters to the surface (Steneck, R. S. et al. 2002). Prostrate kelp, such as those in the genus *Saccharina*, lack a rigid stipe or gas filled buoys (pneumatocysts) and so remain close to the sea-floor (benthos). Stipitate kelp such as *L. setchellii* and *P. californica* are held aloft by rigid stipes and occupy a position higher in the water column. Finally, floating canopy species such as *Macrocystis* and *Nereocystis* (and to some degree *Egregia menziesii*) rely on pneumatocysts to hold the main photosynthetic blades aloft near the water surface. Kelp communities with floating canopies form the most structurally complex forests and provide the greatest volume of habitat for associated species, but diverse assemblages of mid-story and prostrate kelp provide quality refuge and habitat in areas lacking large floating canopies.

Reproductive Ecology

All kelp exhibit heteromorphic life histories of alternating generations (Hurd, C. L. et al. 2014; Schiel, D. R. & M. S. Foster 2006). Kelp alternate between large, asexual, diploid adults called sporophytes and microscopic, sexual, haploid spores (Figure 2). 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, I. et al. 2008a). Other species, such as *Macrocystis* and the locally abundant *A. 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 that often travel long distances on prevailing currents before recruiting (Suskiewicz, M. S. 2010). Generally, kelp zoospores fall within several meters of the parent plant; however, zoospore dispersal distance is still poorly studied with some research suggesting that local current regimes may play a substantial role in connecting isolated populations. Additionally, adult plants, especially *Nereocystis*, when broken free from the benthos, can form floating rafts capable of traveling long distances while continuing to produce viable spores (Rothäusler, E. et al. 2009).

Kelp require hard substrates and will attach readily to both consolidated bedrock and unconsolidated gravel (Dayton, P. K. 1985). Once attached, spores germinate into male and female gametophytes that reproduce sexually to produce a microscopic, germling sporophyte. Following this initial recruitment, juvenile sporophytes grow rapidly throughout the entirety of the growing season. In the Salish Sea, macroalgal recruitment and growth coincides with peak daytime low tides during the spring and early summer (Maxell, B. A. & K. A. Miller 1996b).

Kelp exhibit high growth rates making them competitively dominant in subtidal algal assemblages (Dayton, P. K. 1985). The ability of kelp to quickly recruit to newly cleared substrates contributes to its resiliency. As a result, persistence of any kelp species is partially limited by its ability to recruit to available substrate (Reed, D. C. 1990). Recruitment depends on species-specific life histories and ambient environmental conditions. For example, 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 (Geange, S. W. et al. 2014a). If a large disturbance results in the loss of most adult plants before spore dispersal, recruitment may be severely impacted. Similarly, if microscopic life stages are impacted by abiotic or biotic stress, the population will shift from competition between adults and new recruits to one wholly dependent on adult sporophytes (Wernberg, T. et al. 2010). In these cases, any disturbance that extirpates adult sporophytes may result in total bed loss.

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For all annual species and perennial species with seasonal spore production, there is growing evidence that microscopic forms can remain dormant or overwinter until conditions are favorable for reproduction and growth (Carney, L. T. & M. S. Edwards 2006). Generally, evidence points to gametophytes being the most common life stages capable of overwintering, although there is some evidence that spores and germling sporophytes may overwinter as well (Hurd, C. L. et al. 2014). Controlled laboratory experiments have produced the bulk of evidence for dormancy in microscopic life stages and, while valuable, caution is prudent when generalizing results to in situ populations (Schiel, D. R. & M. S. Foster 2015). One should also assume that the abiotic thresholds and biotic stressors for zoospores, gametophytes, and germling sporophytes differ from those of adult sporophytes and between species. Unfortunately, the cryptic nature of microscopic life stages and logistical difficulties associated with conducting underwater ecological research continues to be the largest hurdles in increasing our understanding of these critical life stages in the field (Dayton, P. K. 1985).

Sediment as Physical Disturbance

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 adult sporophytes, increases in water turbidity can impact photosynthetic performance (Schiel, D. R. & M. S. Foster 2015) and cause significant mortality to kelp spores, gametophytes, and germling sporophytes (Deiman, M. et al. 2012; Geange, S. W. et al. 2014b; Watanabe, H. 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 into the effect of suspended and settled sediments on *Nereocystis* and the dragon kelp *Eularia fistulosa* that is closely related to *Alaria marginata* found in the Puget Sound, suspended sediment loads of 420 mg/L resulted in only 6 percent average spore attachment while settled sediment reduced spore attachment by nearly 99 percent (Deiman, M. et al. 2012). A similar study on *Macrocystis* and *Undaria pinatifidia* (an introduced cousin of *A. marginata*) spore germination suggests that sediment

loads >100 mg/L may be enough to severely impact gametophyte densities (Geange, S. W. et al. 2014b). However, 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, H. 2005).

Whether sediment is an issue for Puget Sound kelp is currently unknown. Observed suspended sediment concentrations (SSC) for the South Basin rarely exceed 2 mg/L (Calloway, unpublished). However, wave action and tidal currents complicate efforts to measure *in situ* benthic sediment accumulation and SSC (Storlazzi, C. D. 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.

Light Availability in Temperate Regions

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, P. K. 1985; Hurd, C. L. et al. 2014). Generally, 1 percent of total irradiance is regarded as the boundary of the photic zone (Bertness, M. D. et al. 2014). However, this boundary depends on the macroalgal species in question and ambient irradiance, which is itself influenced by the timing of low tides, 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 the Puget Sound shows strong seasonal patterns, increasing 10-fold from approximately 127 µmol/m^2/s in December to 1,348 µmol/m^2/s in July (Knapp, C. L., n.d.). The relationship between irradiance and benthic light availability is further influenced by the timing of low tides, which occur during the night in winter and during the day in summer. The shift from night to day low tides occurs in late-winter in February and March. Despite intermediate irradiances (300 to 515 µmol/m^2/s) during late winter, daytime timing of low tides allows for greater light availability for benthic recruiting kelp (Knapp, C. L., n.d.; Druehl, L. D. & S. I. C. Hsiao 1977).

Several studies have observed that this late-winter period of increased light availability coincides with kelp recruitment in the Pacific Northwest (Allen, B. 2016; Druehl, L. D. & S. I. C. Hsiao 1977; Maxell, B. A. & K. A. Miller 1996a). In recent *Nereocystis* out-plant experiments in the Central Basin conducted by the Puget Sound Restoration Fund, Allen (2016) observed that spore, gametophyte, and juvenile sporophyte recruitment began in February and March, peaking in May. Interestingly, successful recruitment of spores and gametophytes occurred only for treatments out-planted in January and February, while only juvenile sporophytes successfully recruited in the March treatment. These results echo similar observations made by (Druehl & Hsiao, 1977) Druehl and Hsiao (1977) in Barkley Sound, B.C. and Maxell and Miller (1996a) at Titlow Beach in the South Basin of Puget Sound and point toward the importance of seasonal cues for *Nereocystis* reproduction. Light availability can also be significantly altered by turbidity in the form of sediment from runoff, river discharge, and phytoplankton blooms.

Kelp beds at the mouth of the Elwha River completely disappeared for several years following the removal of two large dams (Rubin, S. P. et al. 2017). Total sediment flux during the 6-month period of April through September in the 3 years (2012-1014) 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 prior to dam removal but declined dramatically in the first 2 years afterward (Rubin, S. P. 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, the authors attributed the late season recruitment to low sediment fluxes recorded in late summer of 2014 (<500 tonnes/day) resulting in greater light availability to dormant microscopic life stages.

Irradiance and Photosynthetic Performance

Photosynthesis occurs at variable rates over a range of irradiances (Hurd, C. L. et al. 2014). At compensation irradiances, photosynthetic rates match cellular respiration resulting in increased biomass (Wiencke, C. et al. 2006). Kelp sporophytes generally require 2 to 11 μmol/m^2/s to reach compensation

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(Hurd, C. L. 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 (Carney, L. T. & M. S. Edwards 2006; Vadas, R. L. 1972). For example, germling *Macrocystis* sporophytes delay growth at 2 to 3 µmol/m^2/s (Carney, L. T. & M. S. Edwards 2006). Similarly, Vadas (1972) found that only 1 percent of *Nereocystis* gametophytes exposed to irradiances of approximately 2 µmol/m^2/s for 3 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 increases in photosynthetic rates. Saturation irradiances for kelp sporophytes fall between 150 to 250 µmol/m^2/s (Hurd, C. L. 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) (Carney, L. T. & M. S. Edwards 2006; Vadas, R. L. 1972). However, laboratory investigations into the effect of temperature on California *Nereocystis* gametophyte growth rates observed peak gametophyte growth at 77 and 110 µmol/m^2/s between 13 and 17 °C (Tera Corp. 1982). Whether these discrepancies result from differences in methodology or local adaptations of source populations is unknown but highlights the difficulty in accurately describing the reproductive ecology of kelp microscopic life stages from laboratory trials alone.

While light is essential for photosynthesis, photo inhibition occurs when high irradiances and UV exposure lead to cellular damage and tissue death. Photo inhibition for kelp in general occurs between 850 and 1000 µmol/m^2/s with microscopic stages being especially susceptible to UV damage (Swanson, A. K. & L. D. Druehl 2000). However, photo tolerance, like many traits, is species specific with floating canopy species likely adapted to deal with ambient irradiances at the water surface.

Temperature

Over large scales, kelp species are generally distributed along latitudinal temperature gradients (Bartsch, I. et al. 2008a; Hurd, C. L. et al. 2014; Lüning, K. & W. Freshwater 1988). Individual species have unique optimal temperature ranges that differ between alternative life stages (Dayton, P. K. 1985; Harley, C. D. G. et al. 2012; Hurd, C. L. et al. 2014). Temperature optimums vary between species and can be difficult to fully describe as populations adapted to local conditions can acclimate to a wide range of temperatures (Dayton, P. K. 1985; Lind, A. C. & B. Konar 2017).

Cold-temperate *Laminaria* species can survive and reproduce from 0 to 18 °C but grow optimally in the range of 5 to 15 °C (Bartsch, I. et al. 2008a). Similarly, while *Nereocystis* sporophytes can survive at a range of -1.5 °C to 18 °C (Lüning, K. & W. Freshwater 1988), Maxell & Miller (1996) found that Puget Sound *Nereocystis* stipe and blade growth rates peaked in concert with summer temperatures of 13.5 °C. Laboratory studies of Puget Sound *Nereocystis* germling sporophytes and gametophytes showed similar optimal temperature ranges of between 10 and 15 °C (Vadas, R. L. 1972), and 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, unpublished).

Outside of optimal ranges, photosynthetic performance can be augmented by increasing pigment content, reaction centers, and protein complexes allowing for higher maximum photosynthetic rates and yield as long as sufficient nutrients are available (Bartsch, I. et al. 2008a). Yet, maintaining positive growth in the face of temperature stress may leave adult sporophytes more susceptible to other disturbances as photosynthesis rates can only be increased so much before growth is impacted (Wernberg, T. et al. 2006).

Rothäusler et al. (2009) monitored experimental rafts of *Macrocystis* along a latitudinal temperature gradient along the Chilean coast. Rafts were exposed to three temperature treatments (warm, moderate, cool) in the presence and absence of a common amphipod grazer. A majority of rafts in the cool treatment continued to gain biomass regardless of the presence of grazers while rafts in the warm treatment quickly lost biomass regardless of grazing pressure. Only rafts subjected to the moderate

temperature treatments showed a response to the presence or absence of grazing invertebrates, losing biomass when subjected to grazing pressure but gaining biomass in the absence of grazers.

Similarly, adult *Nereocystis* sporophytes exposed to slightly elevated temperatures of 15.9 °C resulted in 25 percent mortality over approximately a month (Tera Corp. 1982). Temperatures exceeding 18 °C quickly resulted in total mortality of adult *Nereocystis* sporophytes. These laboratory results were corroborated by Schiel et al. (2004) when analyzing a 3.5 °C average increase in water temperature in association with an outflow pipe from a power plant in California. Increased temperatures coincided with a 90 percent loss of the midcanopy species *P. californica* and a 97 percent loss of *Nereocystis*. Loss of adult sporophytes is not necessarily antithetical to kelp persistence. As mentioned, kelp is resilient to disturbance, and microscopic life stages show the ability to remain dormant until conditions favor growth. However, elevated temperatures can negatively affect spore production, germination, and reproduction, significantly delaying recovery following disturbance (Schiltroth, personal communication; Wernberg et al., 2010).

Nutrients

Seasonal and geographic variations in nutrient availability influence the productivity and persistence of kelp species (Dayton, P. K. 1985; Schiel, D. R. & M. S. Foster 2006). Kelp species, like other autotrophs, are carbon and nitrogen limited (Dayton, P. K. 1985; Hurd, C. L. et al. 2014). In laboratory investigations of nutrient uptake rates, Ahn et al. (1998) found that *Nereocystis* showed preference for nitrate over ammonia as nitrate uptake rates increased linearly with nitrate additions while ammonium uptake rates peaked at around 10 µM of ammonium. This preference for nitrate holds true for most kelp species (Bartsch, I. et al. 2008b).

Kelp require suitable nutrients to maintain high growth rates. 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, D. R. & M. S. Foster 2015). No information currently exists regarding optimal nutrient ranges for *Nereocystis* and other kelp species found in Puget Sound. 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 the rate of nutrient assimilation rather than to inherent differences in nutrient requirements (Hurd, C. L. et al. 2014).

Nutrient availability often tracks negatively with temperature and thus season (Dayton, P. K. 1985). During the summer, high temperatures interrupt upwelling regimes that transport vital nutrients from deeper waters to shallow coastal areas. Additionally, warm temperatures are associated with large blooms of phytoplankton that can significantly impact nutrient availability, especially in more sheltered, unmixed areas. Puget Sound does not rely on upwelling regimes and, with the exception of the Hood Canal and Whidbey Basins, is by and large a well-mixed system (Ebbesmeyer, C. C. et al. 1988). Washington Department of Ecology nutrient monitoring data track predictable summer decreases in nutrient levels throughout the Puget Sound, but these sampling points are in deep water and may not reflect conditions in the nearshore environment where kelp is most abundant (Berry, H. 2018).

Grazing Pressures

The effects of herbivory on kelp forest systems is well documented in the popular and scientific literature. Kelp forests served as early evidence in support of the keystone predator hypothesis thanks to the interactions between kelp, urchins (*Strongylocentrotus spp.*), and sea otters in Alaska (Estes, J. A. & D. O. Duggins 1995). Urchins, left unchecked by predators such as sea otters, quickly deforest entire kelp beds, creating crowded barrens. Puget Sound hosts healthy populations of several urchin species, but the extent and distributions of urchin barrens is currently unknown.

While the importance of herbivory from conspicuous macrograzers like urchins is critical in understanding kelp forest dynamics (Steneck, R. S. et al. 2002; Dobkowski, K. 2017), the effect of smaller mesograzers, such as amphipods, small crustaceans, and small gastropods, can exert a similar influence (Duggins, D. et al. 2001; Davenport, A. C. & T. W. Anderson 2007; Pfister, C. A. & S. P. Betcher 2017). Oftentimes, 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 grazer abundance of the gastropod *Lacuna vincta* and mortality of *Nereocystis* in the San Juan Islands of Washington State. *Nereocystis* mortality was highest in high flow areas with low *L. vincta* abundances. 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. Pfister and Betcher (2017) observed similar patterns of mortality associated with wave action and grazer damage to stipes of the upper subtidal species *Pleurophycus gardneri* along the coast of Tatoosh Island off the coast of Washington.

There is some 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, E. et al. 2009). *P. producta* preferentially feeds on *Nereocystis*, often straddling the stipe close to the blades (Dobkowski, K. 2017). Anecdotal accounts from local recreational boaters in the Bainbridge Island and Olympia areas often attribute kelp losses to increases in *P. producta* abundances (personal communication). 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 while grazing can quickly extirpate kelp from large swaths of coast, grazing pressure is not an automatic net negative for kelp populations. Grazing, when checked, acts as an important intermediate and ongoing disturbance that may promote increased macroalgal diversity. In Alaskan *Saccharina groenlandica* and *Nereocystis* beds, Duggins (1980) found that kelp diversity decreased over the long term following experimental removals of urchins. In the absence of regular disturbance, the large perennial *S. groenlandica* quickly monopolized the benthos, excluding most other macroalgae.

Algal Competition

Seaweeds compete for available space, light, and nutrients (Dayton, P. K. et al. 1992; Schiel, D. R. & M. S. Foster 2006). Species that recruit to new available substrate first reduce light availability for

understory species (Wing, S. R. et al. 1993; Hurd, C. L. et al. 2014). *Nereocystis,* for example, relies on early recruitment and fast growth rates in order to quickly attain dominance in the canopy where its floating fronds influence light availability below (Springer, Y. P. et al. 2010). Reductions in light availability from floating canopies directly affects understory assemblages, exerting significant control over the structure and composition of kelp forests (Irving, A. D. & S. D. Connell 2002; Spurkland, T. & K. Iken 2011).

There is current concern that in Puget Sound the invasive *Sargasum muticum* may disrupt native algal succession by altering light availability (Britton-Simmons, K. H. 2004). In experiments conducted in the San Juan Islands, Britton-Simmons (2004) documented a 75 percent reduction in canopy species (*Nereocystis*) and a 50 percent reduction in abundance of understory species at sites with *S. muticum* present. The authors attribute these declines to *S. muticum*'s early March growth that blocks light for native species that recruit slightly later in April.

There is also evidence that gametophytes of different species may swamp microenvironments with pheromones that are chemically similar to those of other species (Reed, D. C. 1990). Both medium and high densities of *P. californica* gametophytes impacted recruitment of *Macrocystis* in a field mesocosm investigation into competitive effects on recruitment, but *Macrocystis* had no effect on *P. californica* recruitment (Reed, D. C. 1990).

KELP ECOSYSTEM GOODS AND SERVICES

Kelp forests provide a variety of indirect and direct services for nearshore marine habitats and human coastal populations valued in excess of $500,000 to $1,000,000 annually per kilometer of coastline (Filbee-Dexter, K. & T. Wernberg 2018). As foundation species, kelp stands positively impact community structure by altering the physical environment, influencing interactions between community members, and providing food and nutrient subsidies through high levels of primary productivity (Altieri, A. H. & J. van de Koppel 2014; Miller, R. J. et al. 2018). High production in turn indirectly and directly supports high-level trophic systems that include commercially and economically important finfish species

including rockfish (*Sebastes* spp.) and salmon (*Oncorhynchus* spp.) (Altieri, A. H. & J. van de Koppel 2014). Kelp species also exert a direct influence on their physical and chemical environment, making them powerful ecosystem engineers that offer important benefits for associated communities and help improve adjacent water quality (Altieri, A. H. & J. van de Koppel 2014; Kim, J. et al. 2015a).

Ecosystem Engineering

Kelp forests create conditions for increased community diversity by altering physical conditions within beds (Miller, R. J. et al. 2018; Altieri, A. H. & J. van de Koppel 2014). The structural complexity formed by large kelp beds alter light availability and attenuates current and wave energy within beds (Christie, H. et al. 2009; Duggins, David O. et al. 1990; Gaylord, B. et al. 2007). Reduced benthic light availability along with physical scour from the movement of kelp fronds maintains open patches for seaweed and invertebrate recruitment (Kennelly, S. 1989; Clark, R. et al. 2004). The foundational benefits of kelp beds create facilitation cascades that support high-trophic systems (Altieri, A. H. & J. van de Koppel 2014; Miller, R. J. et al. 2018).

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

In California *Macrocystis* forests, the floating canopy blocks approximately 55 percent of ambient light, creating ideal conditions for light-flexible, mid-story species such as *P. californica* (Clark, R. et al. 2004). Having a second understory canopy level further reduces light so that only 2 percent of total ambient light reaches the benthos. Unlike the *Macrocystis* canopy, these understory canopies form patches separated by open gaps. At a two-canopied northern California forest, 25 percent of total *P. californica* understory area was patch-gaps. These gaps, exposed to intermediate and variable irradiances, support more diverse assemblages of other red, green, and brown seaweeds while excluding light-adapted (shade-intolerant) species such as *Desmarestia* species and weedy, filamentous turf algae that would

otherwise monopolize available space (Clark, R. et al. 2004; Wing, S. R. et al. 1993). Interestingly, Clark et al. (2004) found that the mid-story *P. californica* exerted more of an influence on algal assemblages than the *Macrocystis* canopy because of its patchier distribution and significant reduction to light availability.

The structural complexity, size, and area that large kelp forests and beds occupy also influences the aquatic environment by altering water and particle flows within and around beds (Duggins, David O. et al. 1990; Eckman, J. E. et al. 1989; Gaylord, B. et al. 2007). Large *Macrocystis* stands have been shown to significantly reduce along-shore and across-shore water flows (Gaylord, B. 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 be otherwise quickly swept over the reef. Beneath canopies, understory kelp simultaneously retain particulate matter, block sediment accumulation on the benthos (Duggins, David O. et al. 1990; Eckman, J. E. et al. 1989), and help sweep sediment from the benthos, maintaining access to hard substrates for sessile invertebrate larvae and kelp spores (Arkema, K. K. et al. 2009; Kennelly, S. 1989).

Kelp-derived Carbon in Food Webs

Kelp production provides important food subsidies that may directly sustain high secondary productivity in kelp forests and surrounding ecosystems (Duggins, D.O. et al. 1989; Krumhansl, K. A. et al. 2014). Most herbivorous, kelp-associated macroinvertebrate fauna does not feed directly on fresh kelp tissue. Rather, they ingest kelp-derived carbon in the form of dissolved organic material (DOM) and particulate organic material (POM) (Altieri, A. H. & J. van de Koppel 2014; Christie, H. et al. 2009). The sheer volume of kelp detrital production magnifies sets off bottom-up trophic cascades that are evident through all levels of kelp forest food webs.

In Norwegian *L. hyperborea* forests, kelp primary productivity is three times that of phytoplankton productivity and kelp detritus makes up the bulk of kelp forest POM (Fredriksen, S. 2003). This high productivity leads to increased growth rates for associated sessile and filter feeding

invertebrates. Duggins et al. (1989) found that subtidal mussels (*Mytilus edulis*) and intertidal barnacles (*Balanus glandula*) grew two and four times faster, respectively, within and in proximity to Aleutian Island kelp forests in Alaska. While it is intuitive that filter feeding organisms would stand to gain the most from kelp detrital production, investigations into food web connectivity show that kelp-derived carbon is ubiquitous throughout nearshore trophic systems (Koenigs, C. et al. 2015; Biela, V. R. von et al. 2016).

It is possible to trace kelp-derived carbon through food webs using carbon (∂^{13}C) isotopes as kelp detritus generally has a higher carbon isotopic value than associated phytoplankton (Fredriksen, S. 2003; Miller, R. J. & H. M. Page 2012; Biela, V. R. von et al. 2016). Such analyses consistently demonstrate the significant role kelp-derived carbon plays in subsidizing kelp forest food-webs (Figure X). 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 biomass in some gastropod species (Fredriksen, S. 2003). In Alaskan kelp beds, kelp-derived carbon constitutes 57 percent of muscle biomass in black rockfish *(Sebastes melanops)* and kelp greenling *(Hexagrammos decagrammus)* (Biela, V. R. von et al. 2016).

While these numbers are impressive, a recent review suggests that the contribution of kelp-derived carbon may be overstated as a result of the reliance on offshore phytoplankton for comparative carbon values (Miller, R. J. & H. M. Page 2012). However, Miller and Page point out 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.

Kelp as Habitat, Nursery, and Refuge

The structural diversity and volume of habitat created by kelp assemblages are unique in marine macrophytic communities and lead to high densities of associated fauna (Christie, H. et al. 2009). For example, Norwegian fucoid, a non-kelp macroalgae, and sea-grass assemblages both harbor densities of about 100,000 animals per square meter while nearby kelp communities composed of *L. hyperborea* and

S. latissima contain densities approaching 500,000 animals per square meter (Christie, H. et al. 2009). Long-term monitoring of kelp forests in Channel Islands National Park clearly demonstrates the significant effect of kelp canopies on community assemblages (Graham, M. H. 2004).

Comparisons of species assemblages from healthy *Macrocystis* forests to those in nearby deforested urchin barrens show a 36 percent decrease in species richness across all taxa and significant decreases in overall faunal abundances (Graham, M. H. 2004). Few of the species observed were true kelp forest obligates, but all taxa benefited from the volume of habitat provided by the large *Macrocystis* canopies. While large kelp forests provide the most dramatic volume of habitat, prostrate and smaller stipitate understory kelps also provide critical habitat.

Alaskan understory kelp assemblages support higher diversities and abundances of amphipods, copepods and other macroinvertebrates compared to kelp-free substrates (Siddon, E. C. et al. 2008). This holds true of understory assemblages with and without *Nereocystis* canopy presence, suggesting understory species alone significantly facilitate increased invertebrate biodiversity (Siddon, E. C. et al. 2008).

Faunal richness and abundance associated with kelp beds are tied directly to the structural diversity of kelp habitat. On an individual plant level, a single kelp provides two to three distinct microhabitats: the holdfast, the stipe, and the lamina or blade (Teagle, H. et al. 2017). The holdfast is the most complex microhabitat provided by kelp species. While holdfast morphology, size, and volume of interstitial space varies widely between species, these structures can host approximately 30 to 70 unique species with assemblages dominated by amphipods, copepods, and polychaetes (Christie, H. et al. 2009; Teagle, H. et al. 2017). Stipes and blades on average harbor fewer distinct taxa but support high 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 5 kg/m^2 of fronds, translating to shrimp and amphipod densities of between 20,000 and 40,000 per square meter.

The larger structures that kelp create on a bed-wide scale serve as high quality nurseries, refuges, and feeding grounds for fish, birds, and marine mammals (Carr, M. H. 1994; Munsch, S. et al. 2016; Pérez-Matus, A. & J. S. Shima 2010). While some of the causal linkages between kelp and fish communities are known, most of our understanding is associative and inferred from habitat use and diet preferences described in the literature (Carr, M. H. 1994; Levin, P. S. 1994; Munsch, S. et al. 2016; Shaffer, S. 2004). Causal linkages do exist, but the complexities of fish association with macroalgal beds makes disentangling the specific functional relationships difficult (Munsch, S. et al. 2016; Pérez-Matus, A. & J. S. Shima 2010).

On large scales, kelp distribution explains variation in fish communities well (Pérez-Matus & Shima, 2010, 2010). Initial larval settlement often occurs at the first patch of suitable kelp habitat encountered, regardless of quality, as refuge from predation (Munsch, S. et al. 2016; Shaffer, S. 2004). For many fish species, juvenile survival is linked to growth rates (Duffy, E. J. et al. 2010). The quality of habitat provided promotes increased growth rates for many fin-fish species. The combination of high quality refuge and ample foraging opportunities ameliorate stress responses associated with non-consumptive predator effects (Donelan, S. C. et al. 2017). The high quality nurseries that kelp provide allow for increased growth rates and growth efficiencies, helping increase juvenile fish survival rates (Duffy, E. J. et al. 2010; Donelan, S. C. et al. 2017)

In the Salish Sea, 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 salmon (*Oncorhynchus* spp.) (Doty, D. C. et al. 1995; Duffy, E. J. et al. 2010; Shaffer, A. J. 2000). Young-of-year (YOY) rockfish surveys in Washington and California demonstrate strong associations between YOY rockfish and kelp habitats.

Puget Sound YOY rockfish were found in 56 percent of all kelp stands with floating *Nereocystis* canopies but only 19 percent of eelgrass beds and 15 percent of macroalgal stands without a floating canopy (Doty, D. C. et al. 1995). Observations of juvenile rockfish in central California kelp forests find

YOY rockfish are often the most abundant constituents of the kelp faunal community (Singer, M. M. 1985). Puget Sound and Salish Sea associations are not limited to rockfish species alone.

Surveys of nearshore habitats in the Strait of Juan de Fuca show similar associations between kelp, surf smelt (*Hypomesus pretiosus*), and salmon, particularly coho (*O. kisutch*), which seek shelter in the interior portions of kelp beds and floating kelp rafts (Shaffer, S. 2004). O'Brien et al. (2018) observed similar shelter seeking behavior by cunner fish in Atlantic *S. latissima* beds along the coast of Maine suggesting this phenomenon is common in kelp habitats throughout the world.

Kelp forests, like eelgrass, are important spawning and rearing habitats for forage fish (Essington, T. et al. 2018; Johnson, S. W., n.d.). In Puget Sound, forage fish rely on shallow nearshore environments for spawning and foraging success (Shaffer, A. J. 2000). Large blades and dense foliage provide prey-dense refuges where midtrophic species like forage fish can feed in safety (O'Brien, B. S. et al. 2018). Pacific herring (*Clupea pallasii*) spawn directly onto submerged aquatic vegetation while sand lance (*Ammodytes hexapterus*) and surf smelt (*H. pretiosus*) preferentially aggregate along the edges of kelp beds close to the shore in order to balance foraging opportunities with refuge from predation (Shaffer, S. 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 (Christie, H. et al. 2009; Greene, C. et al. 2015; Siddon, E. C. et al. 2008). Support for large invertebrate and forage fish populations also make kelp forests prime feeding habitat for adult salmon, rockfish, and Pacific cod.

Diet studies of salmon and rockfish early life stages reveal significant shifts in food preference as fish age and grow that are often tied directly to the structure or feeding opportunities associated with kelp beds (Duffy, J. E. & M. E. Hay 1991; Love, Milton S. et al. 1991). Juvenile rockfish, as mentioned, preferentially recruit to floating kelp canopies to take advantage of large abundances of copepods, amphipods and other abundant zooplankton (Love, M S et al. 1991; Singer, M. M. 1985). As juvenile rockfish grow they seek out deeper water and larger prey items, moving to kelp understories before maturing and moving to deeper water (Love, M S et al. 1991). This strategy not only affords juvenile

rockfish the best foraging opportunities, but also minimizes predation from larger conspecifics and other predatory fish that tend to reside in deeper water.

Juvenile salmon exhibit similar strategies, remaining in nearshore vegetated habitats before moving offshore to feed on larger prey as adults (Duffy, E. J. et al. 2010; Shaffer, S. 2004). Marine survival for juvenile salmon is tied closely to size and growth rates. Rapid growth leads to safety from gape-limited predators as well as the ability to tap into larger and more energy-rich food sources (Duffy, E. J. et al. 2010). While in the nearshore, terrestrial and marine invertebrates (specifically amphipods and other decapod larvae) make up the bulk of juvenile Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kitsutch*) diets (Duffy, E. J. et al. 2010; Shaffer, S. 2004). Researchers in Alaska and Washington also documented preferential associations between chum salmon and pink salmon to submerged and floating kelp beds (Johnson, S. W., n.d.; Shaffer, S. 2004). Stable isotope analysis of native Salish Sea salmon species show that nearshore kelp food webs remain important for Chinook salmon (*O. tshawytscha*) and coho salmon (*O. kitsutch*) throughout adulthood (Johnson, S. P. & D. E. Schindler 2009).

Kelp as Nutrient and Carbon Biofilters

Rapid growth make kelp some of the most productive autotrophs in the world with primary productivity exceeding that of cultivated agricultural fields and tropical rain forests (Krumhansl, K. A. et al. 2016). The end result is an estimated primary productivity in excess of 1200 g/cm^2/year (Christie, H. et al. 2009). Such efficient transformation of nutrients and carbon into new biomass holds important implications for the global carbon budget, ocean acidification, and nutrient pollution.

Recent estimations by Krause-Jensen & Duarte (2016) suggest that deep sea deposition and burial of seaweed biomass in nearshore sediments effectively sequesters 173 TgC yr-1. This estimate exceeds that of carbon sequestration from salt marshes, mangrove forests, and seagrass beds combined. While this is no doubt impressive, these are rough estimates based on data from available literature and the authors acknowledge the need for a more detailed analysis of the role of macroalgae in global carbon sequestration. Carbon uptake and oxygen respiration during photosynthesis also make kelp prime

candidates for amelioration of ocean acidification (OA) (Nielsen, K. et al. 2018). However, large

variations in microconditions in kelp beds make estimating the buffering potential of kelp difficult

(Nielsen, K. et al. 2018). While research into both the carbon sequestration and buffer potential of kelp

beds is just beginning to gain traction, the use of kelp for bioextraction of nutrient pollution is better

documented.

Nutrient bioextraction refers specifically to the use of kelp to extract excess nutrients from

eutrophic coastal waters (Kim et al., 2017). However, only a handful of studies have focused on the

potential for monoculture cultivation of *Saccharina* spp. to address issues related to eutrophication (He et

al., 2008; Kim et al., 2015; Xu et al., 2011). Results from research in China and the eastern United States

show promise (Fei, 2004; Kim, Kraemer, & Yarish, 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 in the first 2 meters of surface waters. This number far exceeds the level

(400 mg/m^3) used as a benchmark for nitrogen eutrophication. Similarly, Kim et al. (2015) determined

that seaweed cultivation could remove up to 274,000 mg/m^2 of nitrogen per year from waters in New

York's Long Island Sound.

GLOBAL TRENDS AND CHANGES

Accurately describing long-term trends in global kelp forests is difficult as kelp generally show a

high level of seasonal and interannual variability, more so than is characteristic of other marine

ecosystems (e.g., coral reefs) or terrestrial biomes (Krumhansl, K. A. et al. 2016). Long-term ($\geq$ 20 years)

and regional scale studies provide the best clarity when assessing historical trajectories of kelp forests

(Krumhansl, K. A. et al. 2016; Pfister, C. A. & S. P. Betcher 2017). But a lack of consistent long-term

data sets for subtidal kelp distribution and trends makes any global snapshot of kelp reliant on a small and

scattered sample of short-term studies.

A recent analysis by Krumhansl et al. (2016) of long-term ($\geq$ 2 years) kelp monitoring data shows

declines in approximately 38 percent of global kelp ecosystems (Krumhansl, K. A. et al. 2016). These

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numbers are backed up by locally documented losses in central-northern California, central-northern Chile, southern Peru, Nova Scotia, the Gulf of Maine, the North Sea, the Mediterranean Sea, South Africa, southern and southeastern Australia, and Tasmania. Localized losses can be severe and difficult to reverse (Filbee-Dexter, K. & T. Wernberg 2018; Steneck, R. S. et al. 2002). Changes in the nearshore environment have led to serious losses of kelp in Australia (Connell, S. D. & B. D. Russell 2010; Wernberg, T. et al. 2016) and California (Catton, C. et al. 2016) while Tasmanian kelp forests have been completely lost over the past 10 years (Ling, S. D. 2008; Ling, S. D. et al. 2009). Despite large regional losses, Krumhansl et al. (2016) also found that 35 percent of global kelp forests have shown no change over 50 years. They caution that this could be due to their reliance on sporadic, short-term (<20 year) studies. The authors also warn that kelp monitoring has declined in frequency and extent over the past 5 years, making a strong case for increasing long-term kelp monitoring projects.

Of additional concern is the fact that kelp forests are a model ecosystem for sudden phase shifts toward novel, less diverse states (Krumhansl, K. A. et al. 2016; Scheffer, M. et al. 2001). The two most common shifts occur because of deforestation resulting from unchecked grazer populations and the replacement of structurally complex and diverse kelp beds with weedy turfs of filamentous and short foliose green, red, and brown algae (Filbee-Dexter, K. & T. Wernberg 2018; Krumhansl, K. A. et al. 2016). As a result, while it appears as though one third of global kelp forests have shown no change over the past 50 years, it is difficult to ascertain how close those forests are to collapse (Krumhansl, K. A. et al. 2016).

Range Shifts

Range shifts and contractions as a result of increased temperatures at the margin of species' historical ranges is a common response to increased global temperatures (Harley, C. D. et al. 2006; Harvey, B. P. et al. 2013). In the northern hemisphere, this contraction in range is not as troublesome as there is a large area of coast reaching into the polar-arctic regions (Smale, D. A. et al. 2013). It is expected that reductions in southern distributions will be offset by gains in northern distributions.

Unfortunately, there is less high latitude coastal habitat in the southern hemisphere, meaning that southern hemisphere kelp losses are more likely to result in total extirpation of kelp habitat.

In addition to changes in kelp distributions, changes to faunal ranges are already impacting southern hemisphere kelp beds around Australia and Tasmania (Ling, S. D. 2008; Ling, S. D. et al. 2009). There, oceanic temperature increases are leading to the "tropicalization" of kelp forests as formerly tropical herbivorous fish and invertebrates creep into historically cooler southern waters (Vergés, A. et al. 2016; Wernberg, T. et al. 2016). Normally, these species help clear space for coral in tropical environments and keep kelp from outcompeting coral species, but in kelp forests these grazers negatively impact recovery from disturbances by grazing new recruits before they can establish and reproduce (Wernberg, T. et al. 2016).

Puget Sound is located well away from major range limits for critical kelp species (Dayton, P. K. 1985; Springer, Y. et al. 2007). While range shifts in community assemblages may be an issue elsewhere, it is unlikely that Puget Sound will be impacted.

Overfishing

Overfishing has severely reduced global populations of once abundant marine mammals and finfish (Bourque, B. J. et al. 2001; Ling, S. D. et al. 2009; Steneck, R. S. et al. 2002). These critical predator populations historically acted as top-down controls to grazer populations in a variety of marine ecosystems (Estes, J. A. & D. O. Duggins 1995). Even in kelp forests with a high degree of trophic redundancy (i.e., multiple species filling the same trophic function) the practice of "fishing down the food web" eventually results in a release from top-down controls (Ling, S. D. et al. 2009).

The most well-documented case of such trophic cascades following release from top-down controls comes from the Alaskan Aleutian Islands. There, extirpation of sea otters resulted in urchin population booms that quickly deforested entire island coasts. Overgrazing results in deforested barrens overcrowded with sickly urchins that persist until populations are controlled. While controls often come in the form of a human urchin fishery or the reintroduction of native predator populations, recovery does

not always result in a return to historical conditions (Estes, J. A. & D. O. Duggins 1995; Steneck, R. S. et al. 2002, 2013).

Bottom-up Collapses

On the opposite side of the trophic spectrum, kelp forests in both hemispheres have been replaced by weedy, sediment-laden turf barrens (Airoldi, L. 2003; Connell, S. D. & B. D. Russell 2010; Filbee-Dexter, K. & T. Wernberg 2018; Moy, F. E. & H. Christie 2012). Turf algae include small filamentous and foliose green and red algae that readily outcompete kelp species for available substrate (Connell, S. et al. 2014). Most notably, shifts to communities dominated by turf-forming algae have been recently documented in North Sea *S. latissima* forests (Moy, F. E. & H. Christie 2012), southern Australian *E. radiata* stands (Connell, S. D. & B. D. Russell 2010), and along developed Mediterranean coasts (Benedetti-Cecchi, L. et al. 2001). These shifts have also been noted in Washington State in proximity to Seattle (Heery, E. C. 2017). In almost all cases, shifts to turf-dominated assemblages occur in close proximity to urban centers with increasing populations.

The prevailing hypothesis is that increased nutrient pollution from anthropogenic effluent and sediment from coastal development create conditions more favorable to turf species (Falkenberg, L. J. et al. 2013; Russell, B. D. et al. 2009). These species in turn trap elevated levels of sediment that create negative feedbacks that prohibit recovery of kelp canopies (Airoldi, L. & M. Virgilio 1998).

PUGET SOUND TRENDS AND PRESSURES

Kelp Trends and Monitoring

Strong anecdotal evidence, citizen science surveys, and analysis of historical data support the conclusion that local pressures have significantly impacted kelp canopies of *Nereocystis* in Puget Sound. However, historical assessments of kelp resources in Washington and current monitoring efforts focus solely on *Nereocystis* canopies, leaving a serious gap in our understanding of the remaining 23 Puget Sound kelp species (Mumford, J. & Thomas F. 2007). A lack of quality baseline data makes the task of describing regional trends more difficult as any analysis of long-term trends must rely on navigation maps

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and limited surveys of Puget Sound kelp canopies conducted during the early 20th century (Berry, H. 2018). Contemporary monitoring, meanwhile, suffers from a lack of consistency in monitoring sites, protocols, and application.

Annual aerial surveys of the outer coast and Strait of Juan de Fuca by the Washington Department of Natural Resources (DNR) represent the best long-term monitoring of floating *Nereocystis* and *Macrocystis* canopies for the state. However, these flights incorporate only the portion of Puget Sound along the west coast of Whidbey Island between Admiralty Inlet and the San Juan archipelago (Berry, H. D. et al. 2005). In Puget Sound, current monitoring efforts are limited to citizen science kayak surveys facilitated by the Northwest Straits Commission (NWSC), aerial surveys of the San Juan archipelago, and recent bed mapping in the South and Main Basin by DNR's aquatic vegetation program. Additionally, local residents often offer anecdotal accounts of losses to *Nereocystis* canopies at docks and harbors throughout Puget Sound. When asked about possible explanations, responses vary from increases in kelp crab abundance, losses to important fisheries species, and effects of shoreline development.

Comparisons of long-term aerial photography of the north Olympic Peninsula to kelp surveys from 1911-1912 document decreases in kelp canopy extent and area around Dungeness Spit, Protection Island, and Port Townsend (Pfister, C. A. et al. 2017). Similar comparisons between historical surveys and aerial photography from 2006 suggest possible losses to the eastern coast of San Juan Island (Berry and Mumford, 2011, SSEC) and comparisons of historical surveys, navigation charts, and anecdotal evidence document a near total loss of kelp canopies around Bainbridge Island in the Main Basin. In the South Basin, recent and comprehensive analysis of historical kelp surveys, navigation charts, and incidental kelp observations from habitat and other target species surveys show clear changes to kelp canopy extent (Berry, H. 2018). Both linear extent of kelp canopies and area have declined in the South Basin but increased in the well-mixed waters of the Tacoma Narrows (Berry, H. 2018). DNR is currently working on analyzing historical data in order to parse out *Nereocystis* canopy trends for the Main Basin but has already documented near losses around Bainbridge Island.

Comprehensive inventories of Puget Sound kelp are nonexistent. DNR has taken first steps toward understanding the full extent and area of Puget Sound *Nereocystis* canopies by identifying and mapping all beds in the South Basin during the summer of 2017. Similar inventories are slated for the Main Basin during summer of 2018 along with concurrent efforts to monitor temperature, salinity, light attenuation, and nutrient variability in proximity to Puget Sound kelp beds. DNR has also monitored declines in bed area, depth extent, and kelp health at the Tucksel Point *Nereocystis* bed at Squaxin Island from 2013 to present. However, this is the only bed that has been monitored by DNR over concurrent years.

In addition to DNR's efforts, the NWSC and seven county Marine Resource Committees have implemented protocols for citizen science kayak mapping of *Nereocystis* canopies. Surveys of kelp area in the Strait of Juan de Fuca, Smith and Minor Islands, Cypress Island, and Cherry Point all show decreases in area in 2014. Kelp canopy area recovered in 2015 and 2016 in well-mixed areas, but not at the more sheltered site at Cherry Point. While these preliminary results are promising, relying on volunteer mapping alone is likely insufficient because of staffing and time constraints.

Current assessments of the extent and abundance of kelp canopies are, so far, rarely paired with monitoring of key abiotic and biotic conditions within associated kelp beds. Local conditions play a significant role in the large interannual variability of kelp bed extent and abundance, and Puget Sound encompasses a number of subbasins and reaches with distinct environmental conditions (Ebbesmeyer, C. C. et al. 1988; Krumhansl, K. A. et al. 2016). Thus, causes for declines in one region may not be applicable to Puget Sound as a whole. Furthermore, monitoring protocols are not standardized between organizations making data synthesis and analysis difficult.

Urbanization and Land Use Conversion

As of 2017, the Washington State population had increased over 300 percent since 2010 with considerable growth to coastal areas (Population Trends, Washington State, n.d.). From 2000 to 2017 the Puget Sound region has seen a 26 percent increase in new housing units (Washington Department of

Commerce 2017). Most of this growth has occurred in and around Seattle, Bellevue, Everett, and Tacoma, but above average rural and urban development is occurring in Whatcom, Skagit, Kitsap, and Thurston counties.

Urbanization is associated with predictable changes to the nearshore environment. Nutrient pollution from increased wastewater treatment plant (WWTP) effluent, increased water temperatures, and decreased salinity as a result of freshwater runoff associated with increased impervious surfaces all interact to create novel conditions in urban nearshore environments (Heery, E. C. 2017). Of particular concern for nearshore kelp beds are increased effluent discharges and non-point sources of pollution from runoff.

Current WWTP effluent loads account for 59 percent of annual dissolved inorganic nitrogen (DIN) loads and 81 percent of DIN loads during summer months (Mohamedali, T. et al. 2011). While large-scale eutrophication is not a current reality for Puget Sound, the proportion of DIN associated with WWTP effluent should be a concern. Research from Australia and Europe showed increases in turf algae and decreases to kelp canopies even in non-eutrophic waters (Airoldi, L. & M. W. Beck 2007; Falkenberg, L. J. et al. 2013). Recently, Heery (2017) documented similar shifts to turf algae in proximity to urban areas in the Main Basin of Puget Sound suggesting that similar mechanisms to those documented in Europe and Australia are at play.

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 change in the catchments that empty into Puget Sound impound 37 percent of total drainage area and has converted or resulted in harvest of roughly 50 percent of all lowland forests and wetlands (Pearson, S. F. et al. 2018). Taken as a whole, these changes significantly alter terrestrial nearshore linkages and negatively impact the ability of the landscape to retain water, sediments, and nutrients.

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

Increased sediment loads can have significant impacts to over-wintering microscopic forms of kelp. However, impacts are dependent on the timing of landslide-related sediment deposition as well as the level of exposure at a given kelp bed (Spurkland, T. & K. Iken 2011). Winter sediment pulses could potentially smother overwintering kelp gametophytes and sporophytes while spring sediment pulses could significantly delay recruitment because of increased turbidity. Whether changes in estuarine sediment dynamics impact nearby kelp beds is a concern in Alaska where river sediment loads are heavily influenced by increased glacial melt as a result of climate change. While Puget Sound is less glacially influenced, 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, S. F. 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 connection between lower intertidal sediments and armoring (Dethier, M. N. et al. 2016). However, it is generally recognized that armoring simplifies shorelines and interferes with natural processes that maintain shoreform structures (Pearson, S. F. et al. 2018). Such interference may potentially alter substrate availability for kelp recruitment, but more research is needed in order to understand the links between substrate availability for kelp microscopic stages and shoreline armoring in Puget Sound.

Historic Impacts of Fisheries

Increased commercial and recreational fishery landings in the 1970s and 1980s significantly impacted Puget Sound trophic structure (Harvey, C. J. et al. 2012). Fishing pressure historically focused on finfish as well as urchin, sea cucumber, and geoduck for export markets. The diversity of species targeted for commercial and recreational harvest encompasses nearly the total range of Puget Sound trophic levels from suspension filter feeders to apex predators suggesting the possibility for serious impacts to trophic functionality in Puget Sound (Harvey, C. J. et al. 2012). This trend of "fishing down the food web" is not unique to Puget Sound and often impacts ecosystem resilience by removing entire functional groups from trophic systems.

Fishery landings for most Puget Sound finfish species peaked and plateaued in 1970s and 1980s before significantly declining (Essington, T. 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 recreational walleye pollock (*G. chalcogrammus*) fishery (Gustafson, R. G. et al. 2000). Of eight salmonids found in Puget Sound, four—Chinook salmon (*Oncorhynchus 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 as threatened and endangered, respectively (Essington, T. et al. 2018; National Marine Fisheries Service 2017). Taken as a whole, adult finfish stocks occupy intermediate to top trophic levels, likely making them incredibly important in maintaining healthy linkages within the Puget Sound trophic system (Davenport, A. C. & T. W. Anderson 2007; Menge, B. A. 2000). Grazer abundances are likely to increase in the absence of top-down controls, possibly causing serious harm to Puget Sound kelp resources.

Puget Sound also maintains a sea cucumber and urchin fishery. Negative impacts of increased sea urchin numbers are well documented in kelp forests throughout the world. Whether or not urchin exert strong control over kelp populations in Puget Sound is an open question but is unlikely given persistent harvest pressure from commercial fisheries. Similarly, sea cucumbers are a vital link in marine

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ecosystems, yet their role in Puget Sound is understudied. In fact, little is understood about how changes in trophic structure have altered ecosystem functionality in Puget Sound in general and kelp ecosystems in particular.

Harvest

Washington State does not allow commercial harvest of seaweed or kelp (WA RCW 79.135.410). There is an exception for *Macrocystis* harvest specifically for the herring "spawn-on-kelp" fishery; however, *Macrocystis* does not occur within the boundaries of Puget Sound or the Salish Sea as defined by this review. Recreational harvest of kelp is allowed on state lands and is restricted to 10 pounds per person, but best harvest practices are codified for State Park lands only (WAC 352-32-350). DNR and the Washington Department of Fish and Wildlife (WDFW) publish pamphlets with suggested best harvest practices but are not codified for state tidelands (WDFW, personal communication).

Currently, all but three state parks are closed to recreational seaweed harvest. Fort Ebey, Fort Worden, and Fort Flagler have limited annual openings from April 16 through May 15 (WAC 352-32-350). Harvest pressure is significant enough at Fort Flagler that WDFW temporarily halts shellfish harvest as differentiating between shellfish harvesters and seaweed harvesters becomes too difficult (WDFW, personal communication). WDFW enforcement officials record interactions with recreational harvesters in the intertidal zone but report forms do not include specific sections for noting seaweed harvest (WDFW, personal communication). There are some questions as to the severity of impacts from recreational harvest.

It is known that kelp often recruit to low intertidal zones early in the growing season only to die back as a result of increased photo stress as irradiances increase throughout the summer months (Druehl, L. D. & B. E. Clarkston 2016). The bulk of the reproductively important population remains in the subtidal zone, eventually releasing spores that attach to available substrate in the subtidal and low intertidal zones (Druehl, L. D. & S. I. C. Hsiao 1977). Recreational harvesters can only target individuals in the lower intertidal zone, possibly buffering regional populations against harvest pressure. Assessments

of total subtidal kelp and seaweed inventories are required in order to understand the recreational harvest impacts to kelp.

RECOMMENDATIONS AND DATA GAPS

As a first step toward human recovery efforts, it is necessary to contextualize kelp recovery within a framework that recognizes the role of human activity in shaping and altering nearshore ecosystems. To do so, this plan adopts the European Environmental Agency's DPSIR (Driving Forces, Pressures, State, Impact, Response) framework for action planning (Kristensen, P. 2004). "Driving forces" are needs such as shelter, economic opportunities, and food that lead to "pressures" on the environment from activities such as agriculture, development, etc. These pressures alter the "state" of the environment by altering environmental conditions that in turn "impact" ecosystems structure, function, processes, and services. Using this framework will allow managers to help focus monitoring efforts and identify the most effective leverage points for implementing "responses" (both specific activities that impact nearshore kelp beds and tangible targets for conservation and restoration).

Traditional management approaches often focus on target species and specific impacts to habitats and ecosystems (Long, R. D. et al. 2015). There is growing acknowledgement that a more holistic approach is necessary to maintain resilient and sustainable coastal resources because of the significant failures from traditional management styles (Long, R. D. et al. 2015; Thom, R. et al. 2005). Coastal resource stakeholders are increasingly adopting ecosystem-based management (EBM) principles that focus on more holistic management of ecosystems with consideration to each individual part and their connections. Like the DSPIR model, EBM acknowledges the role of human activity and its ability to negatively and positively influence ecosystems. By nesting the DSPIR model within the broader framework of EBM, this plan aims to foreground human involvement, participation, and stewardship of nearshore kelp beds as core tenets for sustainable and equitable long-term management.

The drivers and pressures at play in Puget Sound have already been discussed at length and their interactions with the state of nearshore marine environments are generally well understood. However,

pinpointing direct impacts to kelp as a result of Puget Sound pressure is difficult because of a lack of adequate monitoring and inventory data. Key gaps in our knowledge of Puget Sound kelp ecosystems in particular are compounded by gaps in our broader understanding of kelp ecology and biology (Table X). The more general gaps in kelp knowledge in turn affect restoration planning and implementation because of uncertainty about the ecology of reproductively important microscopic life stages in the wild.

Table X. Puget Sound kelp knowledge gaps

Topic	Gaps	Available Information[*]
Kelp	- Distribution and trends - Invasive species - Turf assemblages - Trophic contributions - Habitat functions and services - Microscopic life stage ecology (thresholds, delayed development, etc.) - Genetic variation - Bed connectivity - Microbiome - Disease - Competition	- Historic distribution data and charts - Traditional ecological knowledge - Existing underwater towed and drop camera footage - Dive survey data
Kelp Communities	- Invertebrate community and abundances - Fishery impacts - Grazing impacts (urchin, kelp crab, smaller invertebrates) - Salmon, rockfish, and forage fish use	- Dive survey data - Historic fishery data
Ecosystem Services	- Nutrient filtration - Ocean acidification amelioration	Atlantic and California kelp
Kelp Economics	- Fishery contributions - Water quality improvement	Market value of pollution mitigation and cleanup
WA State Policy	- Kelp mariculture permitting - Restoration permitting - Harvest regulations - Conservation regulations	- Eelgrass-associated regulations that mention macroalgae - WDFW enforcement data - State park harvest information

Topic	Gaps	Available Information[*]
Human Impacts	- Shoreline armoring (subtidal effects) - Pollution - Boat traffic - WWTP effluent	- Existing environmental monitoring data available from NOAA, WA-DNR, WA-DOE, and WA-DOT and others. - WWTP discharge data and locations
Restoration	- Site selection - Out-plant methods - Site enhancement - Invasive species management (macroalgae) - Ecosystem services of kelp mariculture	- Nile Creek *Nereocystis* restoration project, British Columbia - Atlantic seaweed mariculture industry

[*] Includes currently available data that may provide possible insight but first requires analysis and synthesis. This section does not include current research by a number of students and researchers in the greater Salish Sea region.

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