From Introduced to Invasive and Iconic: An aquaculture oyster (*Crassostrea gigas*) and social-ecological resilience in Puget Sound

Kathrin (Rina) S. Hauptfeld

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

Master of Marine Affairs

University of Washington
2013

Committee:
Terrie Klinger
Thomas M. Leschine

Program Authorized to Offer Degree:
School of Marine and Environmental Affairs

University of Washington

Abstract

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Kathrin (Rina) S. Hauptfeld

Chair of the Supervisory Committee:
Associate Professor, Terrie Klinger
School of Marine and Environmental Affairs

The resilience framework is increasingly used to understand the dynamics of sustainability in coupled social and ecological systems. Resilient ecological systems exhibit high levels of diversity, including species and habitat diversity, and redundancy, all of which are thought to help maintain the system within a domain of attraction. Numerous studies demonstrate the threat posed to natural systems by the introduction of invasive species on a global scale. Over the past century, biological invasion has caused changes in biological diversity and alterations to the structure and function of ecosystems. In Puget Sound, the non-native Pacific oyster (*Crassostrea gigas*) has been used as a commercial aquaculture species for over a century, despite increasing evidence that its spread threatens ecological resilience of the nearshore system. Interestingly, recent changes in ocean conditions that lessen the invasion threat have been met with alarm in Washington, as they jeopardize the social resilience built on the culture of Pacific oysters. In this case study, I discuss conflicts between social and ecological resilience, and the values that drive those conflicts. I then discuss social adaptation strategies as options to retain social-ecological resilience within the system.

Section 1: Biological Diversity in a Resilient Social-Ecological System

> "We are all part of linked systems of humans and nature."
> (Walker and Salt 2006)

Human societies exist within a coupled social-ecological system in which natural and social systems are interdependent. Humans depend on natural systems for their continued welfare (Levin and Lubchenco 2008). Intact, functional ecosystems provide numerous ecosystem goods and services that contribute to human wellbeing (Chapin et al. 2006, Turner et al. 2003). Changes to the ecological system influence the social system, and vice versa. Disruption of ecological structure and function causes losses to ecosystem services that humans depend on and enjoy (Levin and Lubchenco 2008, Seastedt et al. 2008, Chapin et al. 2006). Safeguarding individual social and ecological systems from undesirable changes helps maintain a social-ecological system. Despite the dependence of social systems on ecological systems, human activities remain the primary drivers behind fundamental and often irreversible changes in the natural systems, eroding ecological resilience (Chapin et al. 2006, Folke 2006).

Sustainability of the social-ecological system is largely determined by the resilience of the system (Levin and Lubchenco 2008, Chapin et al. 2006, Walker and Salt 2006, Tompkins and Adger 2004). Resilience is "the capacity of a system to absorb disturbance and still retain its basic function and structure" Walker and Salt (2006). The ability of social groups to cope with external shocks to their social infrastructure as a result of social, political and environmental change, determines their social resilience (Adger 2000). The resilience of an ecological system relates to the functioning of the system, rather than the stability of its component populations, or even the ability to maintain a steady ecological state (Adger 2000). Greater resilience in a system confers increased capacity to weather sometimes unexpected disturbances without shifting to new states that are less desirable (Walker and Salt 2006, Holling 2001, Adger 2000).

Resilient systems are able to withstand stronger and more frequent disturbances without altering their fundamental structure or function. When the frequency or intensity of disturbance surpasses the ability of the system to resist or recover, it is often difficult, and in some cases impossible to cross back to the previous system (Walker and Salt 2006). The threshold at which systems cross into undesirable states depends not only on the nature of the disturbance, but also on the structural and process attributes of the system (Walker and Salt 2006).

Attributes that confer resilience to an ecological system include high levels of structural and process modularity, redundancy, and diversity (Walker and Salt 2006). Modularity enhances the system's capacity to buffer environmental change by allowing disturbances to be compartmentalized (Levin and Lubchenco 2008). Diversity and redundancy promote stability in ecosystem processes (Levin and Lubchenco 2008, Ruckelshaus et al. 2008, Folke et al. 2005, Hughes et al. 2005) by increasing the diversity of potential responses to disturbance, thereby reducing vulnerability to natural and anthropogenic stresses (Walker and Salt 2006). Species within the same functional group (such as primary producers, grazers, etc.) may be susceptible to different stressors and disturbances such as disease, predation, and desiccation. With greater diversity of species, the likelihood that any particular disturbance will eliminate an entire functional group is reduced.

Loss of biodiversity increases ecosystem susceptibility to abrupt change, which is likely to result in loss of ecosystem function (Worm et al. 2006) and may be both the result and cause of a decline in ecological resilience. To maintain and promote ecological resilience, efforts to "promote and sustain diversity in all forms" must be taken (Walker and Salt 2006). Resilience tends to be greater in systems that maintain native biological diversity, including ecosystem, population, genetic, and species diversity. Because specific disturbances can affect species differentially, maintaining adequate species diversity increases the likelihood of sustaining ecological function in an environment undergoing natural and anthropogenic disturbances such as those associated with climate change, resource exploitation, pollution, habitat loss and invasive species (Millennium Ecosystem Assessment 2005a).

Section 2: Invasive Species Threaten Biological Diversity

Although we depend upon the ecological systems that surround us, “human actions are fundamentally, and to a significant extent irreversibly, changing the diversity of life on Earth, and most of these changes represent a loss of biodiversity” (Millennium Ecosystem Assessment 2005a). Changes in biodiversity are caused by the interaction of demographic, economic, sociopolitical, cultural, and technological drivers. Some stressors are localized, such as habitat destruction. Others stressors are global, such as climate change. Many stressors operate across a continuum of scales; biological invasion is one such stressor (Millennium Ecosystem Assessment 2005a). I use the term invasive species for non-native species that have been introduced, established, spread and proliferated in a geographic range not previously occupied by that species (adapted from Colautti et al. 2006, Vermeij 1996).

Invasions of non-native species are a leading threat to terrestrial and marine biodiversity worldwide (Padilla 2010, Rooney et al. 2007, Walker and Salt 2006, Wonham and Carlton 2005, Park 2004, Vitousek et al. 1996). Although the impacts are often difficult to evaluate (Millennium Ecosystem Assessment 2005a), estimated economic losses due to invasive species total more than US $1.4 trillion annually in losses of biodiversity and impacts to ecosystem service (Burgiel and Muir 2010). By some accounts, the threat posed by invasive species to coastal biodiversity in the marine environment is surpassed only by habitat destruction and over-harvesting (Millennium Ecosystem Assessment 2005a) and rates of invasion are increasing (Weigle et al. 2005).

Invasions by non-native species threaten biological diversity through predation on or competition with native species, altering native habitats, and disrupting community structure and function (Travaset and Richardson 2006). These changes potentially alter the nature and frequency of natural disturbances, further exacerbating negative and often irreversible alterations in native habitats (Seastedt et al. 2008, Klinger et al. 2006, Chapin et al. 1997). Moreover, invasions of non-native species may act in a synergistic fashion with other anthropogenic stressors such as habitat loss, climate change, nutrient loading or pollution (Millennium Ecosystem Assessment 2005a), amplifying their impact. Introduced species have been shown to "facilitate one another's establishment, spread, and impacts", particularly at a population-level (Simberloff 2006, Simberloff and Von Holle 1999), and systems with low diversity may be more susceptible to disturbance than systems with high diversity (Perrings et al. 2002).

Environments are made more vulnerable as the disturbances to which they are exposed increase in size and frequency (Chapin et al. 1997). Aquatic ecosystems are prone to establishment of non-native species (Sousa et al. 2009). In Puget Sound, vectors of biological invasion include hull fouling and ballast water discharge associated with international and regional shipping, escapees from the aquarium trade, and the cultivation of non-native species for food (Wonham and Carlton 2005). Of these vectors, intentional cultivation of non-native organisms has a greater likelihood to result in new communities that establish, reproduce, and spread (Weigle et al. 2005). In addition, early changes to the community may be difficult to detect and quantify, because biological invasions are characterized by a slow colonization period followed by rapid range expansion (Crooks and Soulé 1999). However, once marine invasive species become established, they are nearly impossible to eradicate, and control is often difficult and costly

(Weigle et al. 2005). Repeated and intentional propagation of the non-native Pacific oyster (*Crassostrea gigas*) for commercial and non-commercial harvest represents a risk of biological invasion and subsequent alteration of biological diversity, habitat structure and ecological resilience in Puget Sound.

Section 3: Washington's Case of the Pacific Oyster

Of oysters used in aquaculture, the Pacific oyster (*Crassostrea gigas*) dominates global production (Padilla 2010) and is the dominant aquaculture species in Washington State waters, accounting for more than 80 percent of the state's farmed shellfish harvest and more than 50 percent of total annual sales (Washington State Blue Ribbon Panel on Ocean Acidification 2012). Washington's Pacific oyster production has made it the leading oyster-producing state in the nation. Although few recognize it as non-native, the Pacific oyster was introduced from Japan a century ago (Ruesink et al. 2005). In fact, of all the oyster species[1] now on the West Coast, only the Olympia oyster (*Ostrea lurida* Carpenter 1864, often synonymized with *O. conchaphila* Carpenter 1857) (Polson et al. 2009) is native (Gordon et al. 2001).

Introductions of Pacific oysters to Washington were precipitated by the California Gold Rush of 1849. Dense settlements of miners, prospectors, and boomtown entrepreneurs rapidly grew up in the San Francisco Bay area, creating the demand for a luxurious protein (Gordon et al. 2001). Within two decades, the local beds of native oysters were exhausted, and the market looked northward for sources. A lucrative resource, the native Olympia oyster was aggressively harvested in Washington without consideration or awareness of the oyster's capacity for reproduction. Oysters were shipped still in their shells to the San Francisco area, leaving no culture surface (or "cultch") in local waters for spat to settle upon and grow. Instead, shells were ground up and used as fill in construction and stabilization of roadbeds in California. Within a few short decades, the native Olympia oyster beds in Washington State were reduced to

[1] *Crassostrea gigas, C. angulata, C. sikamea, C. virginica, Ostrea edulis, O. lurida* are found on

economically unsustainable numbers. Despite this bust, the oyster boom was far from over in Washington, and its legacy persists today.

Encouraged by expanding markets for oysters, oyster growers on the West Coast introduced five species of oyster with varying degrees of success, beginning with the Eastern oyster (*Crassostrea virginica*). In 1919, just decades after its introduction, the Eastern oyster was largely decimated by an unidentified disease (Gordon et al. 2001). Despite its brief prominence, the profitability of the Eastern oyster and the decline of the native Olympia oyster (*O. lurida*) ushered in an expansion of attempts to grow non-native varieties in Puget Sound (McNevin 2007). Attempts to introduce the Pacific oyster, which grows to about 30 centimeters (FAO 2005), compared with the native Olympia oyster's five centimeters, began as early as 1902 in Washington (Ruesink et al. 2005), and after repeated attempts, successful populations were established by 1919 (Gordon et al. 2001). Despite requiring marketing campaigns to overcome initial public aversion to its appearance (Gordon et al. 2001), the Pacific oyster is now ubiquitous in regional markets and an iconic part of the Pacific Northwest culture.

Social resilience supporting the sustainability of this new source of seafood and economic income quickly developed. In the few decades following the turn of the century, the oyster industry evolved from a commercial venture dependent on the abundance of wild native populations to an organized industry buttressed by the state government. Washington state passed the Callow and Bush Acts in 1890 and 1895 respectively, permitting private ownership of tidelands for oyster cultivation, and establishing state-operated oyster 'reserves'[2] in 1919. These reserves were created to ensure the persistence of the oyster industry in Washington by producing an ample stock of "seed" oysters, sexually viable adults that produce viable offspring (or seed). Today, the Washington Department of Fish and Wildlife continues to manage public beaches for the recreational harvest of Pacific oysters in Puget Sound, and oyster spat is seeded (sprayed from boats, using water canons) onto public beaches each year.

Initial concerns over oyster introduction focused on limiting the threats to oyster viability, while concerns about the impact of the new oyster on the local systems were minor. Regular shipments of oysters for aquaculture were imported between the 1920s and 1970s, with no risk assessments (Ruesink et al. 2005). Concerns about escape of gametes and proliferation of feral oysters were low. The waters of Puget Sound, which generally remain below the temperature (19˚C) required for oysters to spawn and reproduce in the wild (Pauley et al. 1988), but are sufficiently warm for oysters to grow well, were long thought to present a natural limitation to oyster escape. The Pacific oyster is highly fecund, with females releasing hundreds of millions of eggs each year (Padilla 2010). To reduce the likelihood of noxious invasions, local commercial growers employed genetic manipulation, creating and using sterile triploid adults to inhibit the accidental reproduction of cultured varieties (Ruesink et al. 2005).

[2] Reserves established under Washington State law RCW 77.60.150 and administered by the Washington State Department of Natural Resources in conjunction with Washington Department of Fish and Wildlife.

Despite this, in recent decades, feral[3] Pacific oysters spread unassisted to rocky shores throughout the San Juan Archipelago, Washington, to Desolation Sound, British Columbia (Gillespie et al. 2007), and evidence suggests that they may have presented an invasive risk for much of Puget Sound and Georgia Basin (Kelly et al. 2008, Kelly and Volpe 2007, Klinger et al. 2006, Mills and Padilla 2004). Surveys of Pacific oyster populations in the San Juan Archipelago indicate that oysters of different age classes persist (Klinger et al. 2006), suggesting that discrete settlement events have occurred. Moreover, Mills and Padilla (2004) reported that at least one previous settlement event of oysters onto San Juan shores occurred in the 1960s.

Similar expansions of feral Pacific oysters have been documented on almost every continent in the last decade (Padilla 2010, Ruesink et al. 2005). In 2005, established feral populations of the Pacific oyster were reported from 73 countries worldwide (Ruesink et al. 2005), including areas considered unsuitable to support natural reproduction (Wrange et al. 2010, Diederich et al. 2005). In the Wadden Sea, northern Europe, where waters were also thought too cold to support spawning (Moehler et al. 2011, Wrange et al. 2010), aquaculture cultivation began in 1986, and the first free-living oysters were found just five years later (Eschweiler and Christensen 2011, Diederich et al. 2005). By 2005, the Pacific oyster was firmly established in the wild in the Wadden Sea, and still spreading both in abundance and range northward and southward (Moehler et al. 2011, Diederich 2005). Data on abundance and size-frequency distribution there indicate that recruitment occurred in only about one of every three years, corresponding with years of above-average sea surface temperatures in July and August, when spawning and planktonic dispersal of oysters occurs (Diederich et al. 2005). Even though spawning did not

[3] The designation "feral oyster" is used after Kelly et al. (2008).

occur yearly, successful reproduction every fifth year is expected to be sufficient to maintain the population (Diederich et al. 2005). In the Wadden Sea, substantial portions of the population survived for at least five years, and in Great Britain, adults were still present nine years after closure of an oyster farm (Diederich et al. 2005). Even after mass mortality events, empty oyster shells have been observed to largely remain in place on an oyster bed (Troost 2010). Because Pacific oysters express positive feedback settlement behavior (Kochmann et al. 2008), triggered by the presence of adult oysters and previously settled spat (Troost 2009), the presence of oysters continuously increases the area suitable for their settlement (Troost 2010). With increases in nearshore sea surface temperatures expected to substantially exceed current inter-annual variability in the Pacific Northwest (Mote and Salathé 2010, Kelly and Volpe 2007), successful spawning at irregular intervals could be sufficient to allow feral populations of oysters to perpetuate and expand. Increased sea surface temperature combined with episodic warm-water events may increase the frequency of the formation of warm pockets within Puget Sound and Georgia Basin, creating conditions capable of supporting periodic spawning in areas previously considered too cold (Kelly and Volpe 2007). Sea surface temperature measurements at the Race Rocks lighthouse in the Strait of Juan de Fuca near Victoria, BC indicate a long-term warming trend of 1.0°C from 1950, and analysis of geoduck growth rings indicate that the 1990s experienced the warmest summer waters since the 1840s (Snover et al. 2005). Feral oyster expansion throughout the Strait of Georgia has been associated with unusually warm temperatures in 1932 and 1958, which allowed spawning and dispersal aided by strong currents. More recently, feral and farmed oysters have been documented to spawn in Straits of Georgia most years during late summer (Kelly and Volpe 2007).

Alternatively, reproduction and recruitment of Pacific oysters in the waters of the San Juan Archipelago, Washington, and Cortes Island, British Columbia could indicate that oysters have adapted to reproduction in colder waters (Klinger et al. 2006). Spawning has been observed in British Columbia at 15˚C (Diederich et al. 2005). Populations of the Pacific oyster in Japan show a high degree of genetic variation, and most of this variation appears to have been retained by populations of the Pacific oyster introduced for aquaculture world-wide (Troost 2010), suggesting a genetic base for adaptation. The use of triploidy as a mechanism to prevent gonad formation (Nell 2002) also reduced the likelihood of larval spread. However, depending on the method used to induce triploidy, complete sterility is not guaranteed (Nell 2002). Although the fecundity rate is low, triploid females can produce thousands of fertilization-capable eggs every year (Ruesink et al. 2005, Calvo et al. 2001). Triploid Pacific oysters have been crossed with diploid oysters to produce viable offspring (Guo and Allen 1994). Some triploid oysters can revert spontaneously to diploids, in which case their gametes could be functional (Wilkie et al. 2012, Ruesink et al. 2005). Moreover, only about thirty percent of Pacific oysters farmed on the West Coast in 1999-2000 were triploid (Nell 2002), suggesting that the parent population is far from sterile.

Propagule pressure from extensive and expanding culture of oysters (Troost 2010), combined with an extended planktonic larval period, potentially allows for broad dispersal by Puget Sound and Georgia Basin currents, as has been described in British Columbia, where settlement of oysters occurred 60km from the nearest oyster farm (Diederich et al. 2005).

Where Pacific oysters have settled, substantial population, community and habitat changes, both positive and negative, have accompanied their expansion (Ruesink et al. 2005, Padilla 2010). As feral oysters colonize the rocky intertidal zone in the San Juan Archipelago, they appear to transform the species composition and diversity by displacing native species (Mills and Padilla 2004, Klinger et al. 2006). Oyster densities in the San Juan Archipelago may exceed 90% cover in individual plots (Klinger, unpublished data). Where oysters occur at high densities in the mid-intertidal zone in San Juan Archipelago, depauperate "oyster barrens"[4] occur where the habitat was previously dominated by the native rockweed *Fucus distichus* (Figure 1). Losses in species abundance, specifically the decline of the habitat-forming species like rockweed may cause changes in intertidal habitat that reduce primary production and biogenic habitat provision in intertidal areas. Declines in species richness could also disrupt ecosystem function in the rocky intertidal system in ways that are not yet quantified. Because the ecosystem services that are potentially degraded remain largely unquantified and are not traded competitively, they have no monetary value in the marketplace (Levin et al. 2009), and hence may be undervalued.

The potential for oyster colonization in Puget Sound is not limited to rocky intertidal areas. Pacific oysters have the ability to colonize both rocky and soft bottom habitats (Ruesink et al. 2005), and have impacts beyond their immediate area of colonization. Studies on Cortes Island, British Columbia show that the presence of Pacific oysters in the mid-intertidal zone may impact community structure beyond the oyster bed itself. Where Pacific oysters exist in the intertidal, native eelgrass is typically absent directly seaward of oyster beds (Kelly et al. 2008, Kelly and

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[4] The term *oyster barren* is modeled after the well-known California "urchin-barren", depauperate regions displaying high levels of urchins and substantial reductions in other species (Wilson and North 1983).

Volpe 2007). Oysters have been associated with the absence of eelgrass since 1964 (Kelly et al. 2008). Abundance and diversity of fish and swimming macroinvertebrates is significantly higher in eelgrass beds than those areas directly seaward of oyster beds (Kelly et al. 2008, Kelly and Volpe 2007). Eelgrass may be absent because oysters cause sulphide, which is toxic to eelgrass, to accumulate in the sediments. Feces and pseudofeces produced by oysters during feeding and respiration may cause the formation of hypoxic sediments by supporting sulphate-reducing bacteria that produce sulphide (Kelly and Volpe 2007). If Pacific oysters have similar impacts on eelgrass in Puget Sound, the cultivation of oysters may compromise the ecological resilience of species that rely on eelgrass during their life cycle, such as native threatened salmon.

Pacific oysters are themselves ecosystem engineers (Ruesink et al. 2005, Kochmann et al. 2008, Padilla 2010), and have been demonstrated to cause large impacts, both positive and negative, in systems where they are not native. Pacific oysters alter the thermal environment (Troost 2010). They have been shown to provide thermal refuge for a native limpet, causing it to increase in density and thus increase its grazing effects (Padilla 2010). In this way, the oyster facilitates a native species (Kochmann et al. 2008), precipitating a change in community dynamics. Conversely, Pacific oysters have also been shown to facilitate invasion and expansion of secondary invaders, which occupy the newly formed niche (Lang and Buschbaum 2010). The three-dimensional structure of the Pacific oyster bed traps sediment and restricts water movement in shallow areas (Ruesink et al. 2005, Lang and Buschbaum 2010). Oyster beds can create interstitial spaces that provide protection from predation for some species (Padilla 2010, Eschweiler and Christensen 2011). Individual oysters can settle directly onto other sessile invertebrates (Diederich 2005), resulting in complete overgrowth (Kochmann et al. 2008, Eschweiler and Christensen 2011), and they can compete for food with native bivalves (Ruesink et al. 2005, Troost 2010). Abundance of epibenthic invertebrates has been observed to be negatively correlated with the abundance of Pacific oysters (Wilkie et al. 2012).

Evidence from Puget Sound, Georgia Basin, and coastal systems worldwide indicates that expansion of the Pacific oyster's distribution and abundance can have large impacts on habitat and community composition, many of which are potentially undesirable (Ruesink et al. 2005). Because ecosystem function is "… strongly influenced by the ecological characteristics of the most abundant species, not by the number of species" present, species composition "matters as much or more than species richness when it comes to ecosystem services" (Millennium Ecosystem Assessment 2005b). As a stressor that has significant current and potential impacts, the Pacific oyster presents a threat to ecological functions in some areas of Puget Sound, and in turn threatens other native species and the ecosystem services that we derive from the system as a whole. In this regard, the persistence of Pacific oysters in Puget Sound may represent an un-quantified threat to the resilience of at least some aspects of the Puget Sound system. Concerns over harmful ecological impacts, however, conflict with the beneficial ecosystem services, both real and perceived, of introduced oysters and the human needs that they support.

Oysters in Puget Sound offer opportunities for commercial and recreational harvest and are the source of a prized food. Washington is the top provider of farmed oysters, clams and mussels in the United States (Washington State Blue Ribbon Panel on Ocean Acidification 2012). Annual sales of shellfish grown in Washington exceed $107 million, the estimated total annual economic impact of which is $270 million, from profits and employment at distributors, retailers, seafood and restaurants (Washington State Blue Ribbon Panel on Ocean Acidification 2012). Shellfish growers directly and indirectly employ more than 3,200 people (Washington State Blue Ribbon Panel on Ocean Acidification 2012). Oysters account for more than 80 percent of the state's farmed shellfish harvest, and sales alone of aquaculture oysters from Washington are estimated at 58 million dollars (Washington State Blue Ribbon Panel on Ocean Acidification 2012).

Oysters are known for their water filtration capacity. Oysters filter water both when they respire and feed, and in doing so they remove algal cells and other particles from the water column. This filtration can improve water quality and benefit light limited species (Ruesink et al. 2005). However, because Pacific oysters in Puget Sound and Georgia Basin grow five times faster and feed on larger particles than the native Olympia oyster (*O. lurida*), they differentially remove taxa and alter the composition and dynamics of the phytoplankton community (Ruesink et al. 2005, Troost 2010). They can also reduce the rate of larval survival among taxa with sessile benthic stages (barnacles, mussels, oysters) (Wilkie et al. 2012). In Puget Sound, the Pacific oyster potentially could contribute to the failure of the native oyster, *O. lurida*, to recover. Native oysters have failed to recover in locations where non-native species of oyster have been introduced, perhaps due to the introduction of disease carried by that non-native oysters (Ruesink et al. 2005). Evidence suggests that the Pacific oyster has served as an economic replacement for the native oyster, but is not an ecologically functional replacement (Ruesink et al. 2005).

Consequently, for decades a situation has existed in Puget Sound in which Pacific oysters confer clear economic and societal benefits, as well as ecological benefits with respect to water quality. At the same time, Pacific oysters appear to impose negative impacts on some native species and the benthic communities of which they are a part. Recent evidence, however, suggests this system may be entering a phase of transition. In recent years both natural recruitment and hatchery larval seed production have been severely depressed in the Pacific Northwest (Barton et al. 2012). Hatchery problems began in 2006 (Washington State Blue Ribbon Panel on Ocean Acidification 2012), at which time the decline was attributed to observed high concentrations of the bacterium *Vibrio tubiashii* in hatcheries in Washington and Oregon (Barton et al. 2012). Despite the elimination of *V. tubiashii* from hatchery tanks, repeated failures in subsequent years 2006-2008 indicated that the reproductive failure was due to the chemistry of water entering the hatchery (Welch 2012).

The effects of ocean acidification have been forecast for nearly 30 years (Barton et al. 2012) and numerous studies have now illustrated a pattern of negative response of bivalves to ocean acidification (Barton et al. 2012, Miller et al. 2009, Kurihara et al. 2007). The responses of organisms to rising CO_2 are numerous and include negative effects on respiration, motility, and fertility (Barton et al. 2012). Larval oysters appear to be particularly susceptible to the influences of corrosive seawater chemistry, because their shell is formed from aragonite, a more soluble form of calcium (Barton et al. 2012). Studies suggest that effects of ocean acidification during egg development may carry over and affect survival at larval midstage between 120 to 150 micron shell length, after larvae have exhausted egg yolk reserves, and experience high energetic costs of development and metabolism (Barton et al. 2012) and before oysters deposit the less soluble calcite, following settlement.

The upwelled water along the Washington coast takes decades to transit from the point of subduction where it was last exposed to the atmosphere and to anthropogenic CO_2. Recent work by Feely et al. (2008, 2010) indicate that upwelled waters carry an increasing load of anthropogenic CO_2, with the consequence that they are increasingly corrosive to calcium carbonate structures. This threatens not only oysters in Washington, but other shellfish whose calcareous structures are largely composed of aragonite (Barton et al. 2012). Under conditions of ocean warming plus ocean acidification, it's possible that spawning will continue but larval survival of farmed and feral oysters will decline.

In response to the substantial mortality of oyster larvae in hatcheries between 2005 and 2009, Washington State Governor Christine Gregoire convened the Washington State Blue Ribbon Panel on Ocean Acidification in February of 2012, to address the regional impacts of ocean acidification. The 'Blue Ribbon Panel' was assembled under the auspices of the Washington Shellfish Initiative, a regional partnership established to implement the National Oceanic and Atmospheric Administration's Shellfish Initiative. In response to the Blue Ribbon Panel's recommendations, Governor Gregoire issued Executive Order 12-07 directing Washington State agencies to implement their recommended Panel's Key Early Actions (KEAs), including provisions to "enhance resilience of native and cultivated shellfish populations and ecosystems on which they depend" (Washington State Blue Ribbon Panel on Ocean Acidification 2012).

Section 4: Resilience of what, and for whom?

> "At the heart of resilience thinking is a very simple notion – things change – and to ignore or resist this change is to increase our vulnerability and forego emerging opportunities" (Walker and Salt 2006)

A clear link exists between social and ecological resilience for social groups that are dependent on environmental resources for their livelihoods (Daw et al. 2009, Adger 2000). The coevolution of social and natural systems is especially clear among groups that specialize economic activities on one or few resources (Adger 2000), such as aquaculture. However, Gibbs (2009) highlights that context is critical in determining resilience targets and reducing vulnerability as a practical matter. Rather than achieving resilience of the social-ecological system as a whole, social groups are often concerned with the resilience of something particular in the face of a specific perturbation, over a certain timescale (Gibbs 2009). Given the "importance of Washington's shellfish and marine resources to the regional and national economy", Washington has prioritized the "resilience of native and cultivated shellfish populations and ecosystems on which they depend" to the effects of ocean acidification (Washington State Blue Ribbon Panel on Ocean Acidification 2012). A change in ocean condition (e.g., ocean acidification) has reduced the vulnerability of the ecological system to invasion of the Pacific oyster and associated threats, while substantially increasing vulnerability in the social system due to negative impacts on the aquaculture industry. Ocean acidification has converted the Pacific oyster from stressor to casualty, illustrating that human valuation of resilience attributes evolve over time, and in response to a changing social and ecological context.

Recognition of the threats that the Pacific oyster posed to the ecological resilience of the nearshore system in Puget Sound was slow to materialize, in part because of the contribution oysters make to social resilience. Resilience of both social-economic and biophysical systems is inherently a social issue (Gibbs 2009), and because managing for optimized production of a valued aquaculture commodity "promotes the simplification of values to a few quantifiable and marketable ones" (Walker and Salt 2006) it involves de facto tradeoffs of one kind of resilience for another. Unlike most marine invasive species, Pacific oysters were intentionally introduced for their food production value, and have been cultivated throughout the last century for both their use and non-use values, becoming emblematic of the Pacific Northwest. Not only does the Pacific oyster support a lucrative regional aquaculture industry, it contributes to regional human wellbeing through provision of recreational and esthetic values. It is a widespread summer tradition for residents and tourists to harvest oysters that are seeded onto public beaches by state agencies[5] to grow "naturally" in the environment. The public in Washington is acculturated to the presence of oysters on beaches and in restaurants, and may not be aware of its historic introduction, spread and ecological impact, or even that it is non-native.

Awareness of the Pacific oyster's ecological history, however, will not likely translate into reduced veneration for its role in northwest culture. Cultural models may have developed in Washington, as in the Chesapeake Bay region, in which oysters acquire highly symbolic value for their ecological, economic and cultural significance (Paolisso and Dery 2010), as well as their part in history and heritage (Paolisso 2007, Paolisso and Dery 2010). Cultural models are "shared implicit and tacit understandings about how the world works" by various stakeholders,

[5] Washington Department of Fish and Wildlife

including those that work with, manage or consume oysters, that affect human behavior through their ties to emotion (Paolisso and Dery 2010). The presence and cultivation of Pacific oysters in Washington State waters for over a century has firmly ensconced it as part of regional tradition, reflected by local news coverage of the oyster aquaculture failure in emotional terms tied to tradition. The newspaper's cultural framing of an aquaculture producer as a "third-generation oysterman" whose interest in maintaining oyster culture is for the sake of his son (Welch 2012a) illustrates the cultural notions of tradition attributed to oyster production activities in Washington.

The Pacific oyster is now cast as the iconic symbol for the massive threat of ocean acidification. Ocean acidification threatens both social and nearshore ecological resilience in Washington, increasing regional vulnerability, with no clear remedy. Following Chapin et al. (2006), strategies that reduce vulnerability and enhance human adaptability could promote social-ecological resilience in Puget Sound and Georgia Basin. Any meaningful decision to reduce vulnerability and support resilience requires not only widespread support from the public and relevant agencies (Millennium Ecosystem Assessment 2005a), but a political structure able to address the scope of the problem (Levin et al. 2009, Chapin et al. 2006). Formation of the Washington State Blue Ribbon Panel on Ocean Acidification provides evidence that governance in Washington is evolving to address new problems that impact the resilience of a natural resource on which the social system depends. Before leaving office, Governor Gregoire drafted a biennial budget for 2013-2015, calling for the allocation of $3.1 million to pursue key actions in response to the impact that ocean acidification has recently had on Washington's shellfish production, to ensure the continued survival and profitability of the shellfish industry. This initiative appears to be moving forward under Gregoire's successor, Governor Inslee's administration.

Absent technical fixes as proposed by the Blue Ribbon Panel, resilience can be addressed primarily through adaptation (Liu et al. 2007, Armitage and Johnson 2006, Chapin et al. 2006, Folke 2006). Adaptation is an "active set of strategies and actions taken in reaction to or in anticipation of change by people in order to enhance or maintain their well-being (Goulden et al. 2013). Adaptation strategies in response to ocean acidification impacts on oyster cultivation can generally be categorized at three levels of accommodation: technical, government, and social accommodation. Commercial shellfish companies in Washington have begun adapting to the larval mortality caused by corrosive waters by drawing upon the state-run oyster "reserves", established in 1919, to subsidize seed oysters (Welch 2012a) and maintain the resilience of their industry. Hatcheries that produce seed oyster have been allotted congressional funds to re-plumb facilities to avoid intake of corrosive upwelled water, as well as to develop more intensive monitoring systems to track upwelling events and quality of intake seawater (Welch 2012a). The Nisbet Oyster Company in Willapa Bay has opted to sidestep corrosive waters in Washington entirely, instead moving part of its business to Hawaii, where the same upwelling events do not occur, and acidification does not yet appear to be a problem (Welch 2012b). This may be the first business in the Northwest to relocate in response to climate change (Welch 2012b).

Alternatively, adapting future efforts in aquaculture and seeding technology to focus on the native Olympia oyster, instead of the non-native Pacific oyster (Ruesink et al. 2005), could also promote restoration objectives, potentially promoting both ecological and social resilience. Such a fundamentally adaptive approach would require sacrifices by sectors of the community at least in the short term (Gibbs 2009) while nurturing alternate tastes and attitudes. Cultural framing can change public attitudes and values, and Pacific Northwest culture already places high value on other local and wild resources. After all, oyster producers were faced with a similar problem a century ago when attempting to overcome consumer hesitancy about then unknown Pacific oyster that was brought in to alleviate the impact of the crash of the Olympia oyster.

Figure 1. Where Pacific oyster density is high in the rocky intertidal on San Juan Island, "oyster barrens" (top) form depauperate communities compared to the communities in the intertidal zone commonly dominated by the macroalga rockweed (bottom). (Photo credits: T. Klinger)

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