

Introduction

Oyster Filtration Functions

In estuaries along the North American Pacific coast (NAPC), the Olympia oyster, *Ostrea lurida*, is a foundation species that autogenously creates complex three-dimensional habitat (Dayton 1972). The shells of living and dead oysters provide habitat for a variety of invertebrates (Kimbrow & Grosholz 2006, Rodney & Paynter 2006, Ramsey 2012, Boyer et al. 2017), nursery, refuge, and foraging habitat for fishes (Peterson et al. 2003, Coen et al. 2007, Stunz et al. 2010), and foraging habitat for birds (Galtsoff 1929, Boyer et al. 2017). *O. lurida* and other bivalves that recruit to oyster habitat are suspension feeders that remove particulate matter (seston) from the water column and deposit mucus-bound feces and pseudofeces (i.e. biodeposits) on the sediment surface (Elsey 1935, Baird & Ulanowicz 1989, Dame 1999, Kellogg et al. 2013). This feeding behavior contributes to three critical ecosystem functions including nutrient sequestration, trophic energy transfer, and water clarification. Most of the seston particulate organic matter (POM) is ingested by bivalves for growth and maintenance. Nutrients incorporated into bivalve shells can be sequestered long-term (Kellogg et al. 2013) when buried in sediments (Hu et al. 2011), and likely serve as a sink for anthropologically produced nutrients (Martinetto et al. 2006, Carmichael et al. 2012). Bivalve feeding is an important biochemical pathway, linking the water column to the benthos, that transfers energy to higher trophic levels (Kautsky & Evans 1987, Rodney & Paynter 2006) and supplies nutrients to benthic seagrasses (Peterson & Heck 1999). Bivalve biodeposits can have higher organic and nitrogen content than particles settling out of the water column (Kautsky & Evans 1987, Muschenheim 1987), providing high quality food for deposit feeders and subsequently feeding omnivores and carnivores including fish (Rodney & Paynter 2006). Lastly, seston removal via bivalve filter feeding increases water clarity (Newell & Koch 2004, Grizzle et al. 2008, 2018) and, thus, the amount of photosynthetically available radiation reaching benthic primary producers, such as seagrasses (Newell & Koch 2004) and microalgae (Newell et al. 2002).

At a regional scale, the capacity of *O. lurida*'s filtration functions was diminished when *O. lurida* populations were decimated in the late 1800s and early 1900s by destructive fishing practices (Kirby 2004), introduction of non-native species (Bonnot 1935), pollution, and excessive sedimentation (Nelson 1909, Gilbert 1917, Lotze et al. 2006). Currently, *O. lurida* populations are less than 10% of historical abundance in parts of the Pacific Northwest, and less than 1% in the rest of its geographic range (Beck et al. 2011, Ermgassen et al. 2012). The extreme reduction of native *O. lurida* abundances and, therefore, the important estuarine habitat *O. lurida* creates, is likely coupled with the loss of water filtration functions. Restoring filtration functions is one motivation behind native *O. lurida* restoration and living shoreline projects efforts along the West Coast, along with restoring other habitat functions such as habitat provision and sediment stabilization

(Dinnel et al. 2009, Henderson et al. 2015, Latta & Boyer 2015, Wasson et al. 2015, Zacherl et al. 2015). Restoring the filtration functions of *O. lurida* habitat is relative to the mudflats where restorations are often located, which have their own filtration functions driven by infaunal bivalves.

Dwindling *O. lurida* harvests led to the cultivation of the Japanese oyster, *Crassostrea gigas*, (Beattie et al. 1982) in the Salish Sea in the early 1920s (Quayle 1988), and in California in 1928 (Conte & Dupuy 1982). *C. gigas* now accounts for the overwhelming majority of commercial oyster harvest on the NAPC (Beattie et al. 1982, Pauley et al. 1988), and has established feral populations outside of aquaculture operations in the Salish Sea (Quayle 1988), Willapa Bay, Washington (Kincaid 1968), and southern California (Polson & Zacherl 2009, Crooks et al. 2015, Tronske et al. 2018). *C. gigas* is a large, fast growing oyster with higher filtration rates than *O. lurida* per unit dry tissue weight (DTW) (Bougrier et al. 1995, Ermgassen et al. 2013, Gray & Langdon 2018, 2019), and it can exert top-down control of seston at aquaculture densities (Wheat & Ruesink 2013). Furthermore, *C. gigas* has a higher particle capture efficiency presumably because it has smaller gill ostrea than *O. lurida* (Elsey 1935, Gray 2016, Gray & Langdon 2018). Beyond differences in species physiology, many aquaculture operations cultivate oyster in off-bottom structures that are fundamentally different than natural oyster reefs and may alter how commercially grown *C. gigas* delivers pelagic seston resources to benthic communities. Therefore, ecosystem filtration functions (e.g. nutrient sequestration, sediment enrichment, and water clarification) and habitat quality in NAPC estuaries may differ between native *O. lurida* habitat and cultivated *C. gigas* aquaculture (Ruesink et al. 2006, reviewed by 2005).

Single-species Research

Estimating the filtration capacity of *O. lurida* habitat and *C. gigas* aquaculture currently relies on a handful of single-species studies (Ermgassen et al. 2013, 2016, Gray & Langdon 2018, Gray et al. 2019) and a single field aquaculture study (Wheat & Ruesink 2013). Gray & Langdon (2018) estimated the clearance rates of *O. lurida* and *C. gigas* under a range of laboratory and seasonal *in situ* conditions using the biodeposition method (Hawkins et al. 1996). These models provide important insights into the feeding responses of individual *O. lurida* and *C. gigas* to specific conditions (temperature, salinity, turbidity, chlorophyll α , total particulate matter (TPM), and organic content (OC)), but may not be appropriate for estimating whole-habitat clearance rates in the field (Cranford et al. 2011, Grizzle et al. 2018) because they do not incorporate local habitat or hydrodynamics conditions. For example, non-oyster filter feeders living in *O. lurida* habitat, contribute to the overall filtration capacity of the habitat (Grizzle et al. 2008, 2018, Byers et al. 2014, Gedan et al. 2014). These non-oyster filter feeders that occupy oyster habitat have species-specific feeding behavior (Møhlenberg & Riisgård 1979, Riisgård 1988, Riisgård & Larsen 2001, Cranford et al. 2011, Gedan et al. 2014, Gray

2016). The regional composition of this filter feeding guild is likely to change along the NAPC, consequently creating unique filtration signatures for different *O. lurida* habitat. In addition, clearance rates calculated based on biomass are not particularly useful in assessing whether restored *O. lurida* habitat is also restoring filtration functions unless species-specific allometric relationships are known and applied to estimate biomass, as restoration practitioners are hesitant to sacrifice bivalves to measure biomass directly.

Whole-Habitat Measurements

The complex biological and physical characteristics of oyster habitat highlight the need for *in situ*, whole-habitat filtration measurements (Grizzle et al. 2008, 2018, Byers et al. 2014, Gedan et al. 2014) specific to the habitat. Whole-habitat *in situ* filtration measurements have several distinct advantages over single-species measurements. First, *in situ* measurements include the contributions of the entire filter feeding guild. Next, individual bivalve feeding variation is aggregated with a higher precision in *in situ* measurements than filtration rates derived from individual bivalve feeding trials (Iglesias et al. 1998, Cranford et al. 2011, Jones et al. 2011). Filtration studies often exclude individuals that are not filtering (closed valves), and artificially inflate filtration models and overestimate filtration when extrapolated to the population level (Harsh & Luckenbach 1999, Cranford et al. 2011); this may partly explain why many field studies find lower filtration rates than laboratory studies (Newell et al. 2005, Grizzle et al. 2008, Cranford et al. 2011). Lastly, bivalve feeding responses to natural water flow dynamics along with spatial and seasonal changes in seston composition are inherently included in whole-habitat *in situ* measurements.

Water flow dynamics in the field are highly variable (Wilson-Ormond et al. 1997) due to the interaction of tidal prisms and the physical characteristics of bays and estuaries (Dame 2012). Whereas the direct effects of water velocity on bivalve filter feeding is unclear (Grizzle et al. 1992, Cranford et al. 1998, also see review in Judge et al. 1992), water velocity and depth affect water column mixing and sediment re-suspension (Widdows et al. 1998), and thus, food availability for benthic filter feeders. The quantity, particle size, and organic content (OC) of seston available can affect filter feeders' feeding behavior (Cranford & Hill 1999, Newell et al. 2005, Velasco & Navarro 2005, Gray & Langdon 2018, 2019, Moody & Kreeger 2020a b). Natural seston is composed of phytoplankton (Navarro & Thompson 1995), zooplankton (Lehane & Davenport 2006, Trotter et al. 2008), macroalgae detritus (Kwak & Zedler 1997, Page 1997, Gilbane 2006), bacteria (Newell et al. 1989), and inorganic sediments (Wilson-Ormond et al. 1997, Gray & Langdon 2018). Although Gray & Langdon (2018) used ambient sea water from Yaquina Bay, Oregon in their *in situ* experiments across seasons; seston also changes spatially and temporally due to tides, wind, bathymetry, and proximity to benthic organisms (Muschenheim 1987, Ashley & Grizzle 1988, Navarro & Thompson 1995, Moody & Kreeger

2020a), limiting their findings to bays with similar seston profiles.

Cranford et al. (2011) conducted a meta-analysis of 133 bivalve clearance rate studies and found highly variable short-term fluctuations in clearance rates, as well as intermittent feeding cessation when bivalves were fed with natural seston. This illustrates bivalves' highly variable feeding responses to natural conditions, further making the case that whole-habitat *in situ* measurements are needed for ecologically and environmentally realistic filtration estimates of *O. lurida* habitat and *C. gigas* aquaculture.

Research Questions

Here, I assessed the contributions of restored *O. lurida* habitat and *C. gigas* aquaculture to estuary filtration functions in California, as a function of natural water quality conditions and filter feeder communities, which are expected to vary among locations. My research questions were: 1) Do oyster habitat clearance rates (HCR) differ from adjacent mudflat habitat HCR? 2) How do the HCRs of restored *O. lurida* habitat compare to *C. gigas* aquaculture? 3) What biotic and abiotic factors are important in estimating HCR? 4) Is there a predictable allometric relationship between *O. lurida* shell length and dry tissue weight, allowing for accurate estimates of DTW without sacrificing restored oysters?

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