Aquatic Invasive Species Profile

Pacific oyster, *Crassostrea gigas* (Thunberg, 1793)

Jill Harris
Aquatic Invasion Ecology
December 2008

Figure 1. Pacific oyster, *Crassostrea gigas*. Photo by North Island Explorer.

Figure 2. *C. gigas* compared to native Olympia oysters, *Ostreola conchaphila*. Photo by Anne Shaffer, Washington Sea Grant.

Introduction

The Pacific oyster is the most cosmopolitan of all oyster species. It was intentionally introduced to dozens of countries for aquaculture purposes, and it now dominates global shellfish aquaculture production. As an ecosystem engineer, the Pacific oyster can dramatically alter its environment in ways that both benefit and harm native species and ecosystems. It is a unique non-native species because it is extremely valuable to humans, yet has some deleterious effects on important coastal ecosystems. It is the focus of much research and as we learn more about the culture of Pacific oysters, we find ways to reduce its negative ecosystem impacts while ensuring adequate production for growing aquaculture demands.

Diagnostic and identification information

The Pacific oyster, *Crassostrea gigas*, is a common oyster species that grows individually or in dense mats on rocks and soft substrates in temperate tidal and sub-tidal zones (Hughes 2008). It is most easily identified by its blue-gray shell with highly fluted edges (Fig. 1). Internally, the shell is white with a dark purple muscle scar (Hughes 2008). It is much larger, flatter, and has a more crenulated shell than the native Olympia oyster, *Ostreola conchaphila* (Fig 2).

Scientific name

Order: Ostreoida
Family: Ostreidae
Genus: *Crassostrea*
Species: *gigas*

Common names

Pacific oyster
giant Pacific oyster
Pacific cupped oyster
Japanese oyster

These oysters are also marketed under other names based on where they are grown for commercial harvest. For example, *C. gigas* is sold as the Little Skookum oyster when grown in Little Skookum Inlet, Washington.

Life-history and basic ecology

The Pacific oyster grows on intertidal or shallow subtidal areas on both hard and soft substrates. Larvae are planktonic for 20-30 days before settling and attaching to the substrate (Shatkin *et al.* 1997). *C. gigas* are protandrous hermaphrodites: they develop as males and after their first year mature as either male or female (WSG 2002). Pacific oysters grow rapidly and reach 10-15 cm after 2-4 years (WSG 2002). Oysters spawn annually in warm months, and this naturally-produced seed is an important input for commercial aquaculture operations (WSG 2002). *C. gigas* is one of the most fecund of all oysters. During spawning season, over

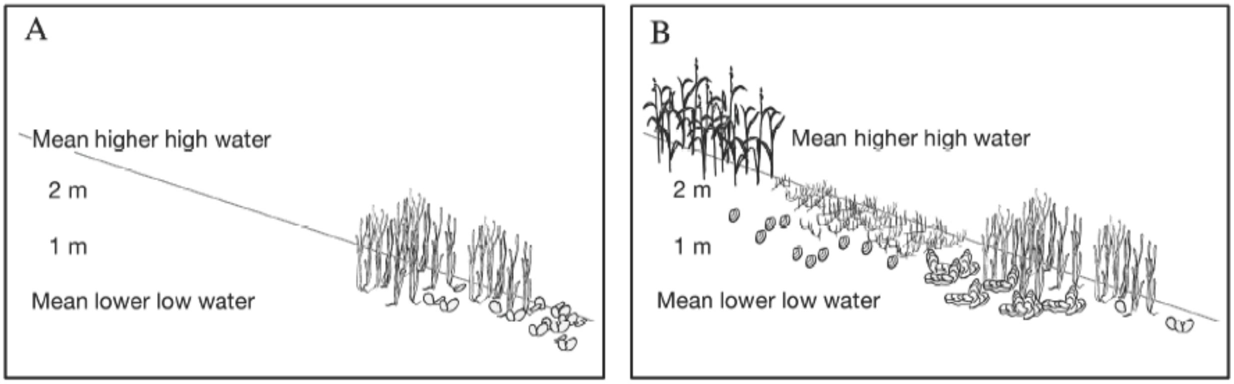

Figure 3. Dominant species on tideflats in Willapa Bay, Washington. A: Before 1900, tideflats were dominated by native eelgrass *Zostera marina* and native oysters *Ostreola conchaphila*. B: Today, tideflats are dominated by invasive grass *Spartina alterniflora*, invasive clam *Ruditapes philippinarum*, invasive eelgrass *Zostera japonica*, invasive oysters *Crassostrea gigas*, in addition to *Z. marina* and low densities of *O. conchaphila* (Ruesink *et al.* 2006).

50% of its body mass is devoted to reproductive capacity (Shatkin *et al.* 1997).

Pacific oysters are hardy filter feeders that can tolerate a broader range of temperature and salinity than native oysters (Ruesink *et al.* 2006), making them extremely desirable for commercial culture and extremely successful at invasion. They thrive in temperatures ranging from 8-22°C (Shatkin *et al.* 1997), though scientists have induced short-term thermal tolerance up to 43°C (Shamseldin *et al.* 1997). They grow best in water with salinity between 24 and 28 ppt, but can tolerate low salinities (down to 5 ppt) for short periods (Shatkin *et al.* 1997). These wide tolerances enable *C. gigas* to grow in a variety of environments that are unsuitable for native oyster species.

This broad environmental tolerance allows *C. gigas* to grow higher in the tidal zone than native oysters grow. A recent study examined spatial distributions of native and non-native species Willapa Bay, WA, an area with a large established population of Pacific oyster (Ruesink *et al.* 2006). Before *C. gigas* was established, native eelgrass *Zostera marina* and native oysters, *Ostreola conchaphila*, dominated the lower portion of the intertidal zone, and areas above high tide were mostly uncolonized (Fig 3A). Today, *O. conchaphila* is only found in very low densities, while C. gigas and associated non-native species dominate tideflats (Fig 3B).

Current geographic distribution

Global distribution

The Pacific oyster is the most cosmopolitan of all oyster species. It has been introduced to 66 countries and has successfully established in 17 countries (Fig 4, Ruesink *et al.* 2005). Prior success of invasion is one characteristic used to predict species that will become invasive in other contexts; based on its global distribution

Figure 4. Global distribution of the Pacific oyster, *Crassostrea gigas*, in its native and non-native ranges. Red = native range, blue = established populations, green = introduced but not established outside aquaculture (Ruesink *et al.* 2005).

and history of invasion, *C. gigas* certainly displays this trait. It can adapt to a wide range of environments and inhabits most temperate coastlines of the world, in both the Pacific and Atlantic Oceans.

Domestic distribution

In the United States, *C. gigas* grows primarily on the west coast, though it is also grown in small numbers along the north Atlantic coast. It grows along the entire Washington coastline, with high populations throughout Puget Sound and the mouth of the Columbia River (Fig 5). A recent survey found high population densities of *C. gigas* inside the boundaries of marine reserves on San Juan Island (Klinger *et al.* 2006), indicating that other coastlines beyond the reach of human impact may also host *C. gigas* populations. Populations of *C. gigas* are also found further south, along the Oregon and California coasts, and further north, along Vancouver Island and the coasts of British Columbia and Alaska (Fig 5).

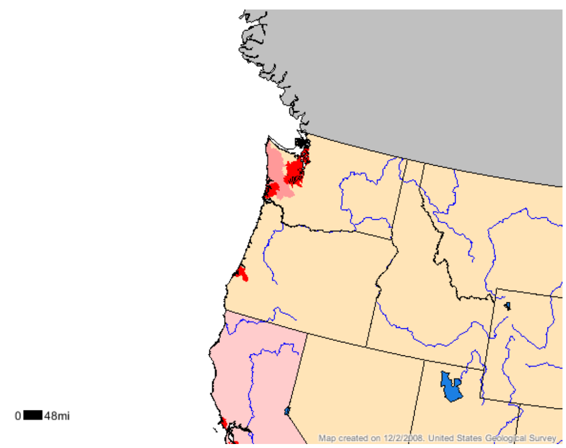

Figure 5. Distribution of the non-native Pacific oyster, *Crassostrea gigas*, in the Pacific Northwest. Red and pink areas indicated established populations (source: USGS Nonindigenous Aquatic Species Database).

History of invasiveness

The Pacific oyster is native to Japan and coastal regions of Asia. After populations of native Olympia oysters, *Ostrea conchaphila*, declined in Washington State, *C. gigas* was introduced for aquaculture purposes (Shatkin *et al.* 1997). The Pacific oyster was first introduced to Washington in 1902, and when culture proved to be successful, regular shipments of oysters began in the 1920's (Shatkin *et al.* 1997, Ruesink *et al.* 2005). The first successful broodstock was produced in several locations in 1936, including Hood Canal and Willapa Bay (NRC 2004, Ruesink *et al.* 2005). Deriving seed from local stocks was more efficient and reduced the chance of importing diseases, so direct shipments from Japan to Washington slowed in the 1970's when hatchery production took over (Ruesink *et al.* 2005). Today, most of Washington's oyster industry is based on hatcheries rather than shipments of adults (Shatkin *et al.* 1997).

Invasion Process

Pathways and Vectors

Aquaculture is the primary pathway for the introduction of Pacific oysters to Washington. Introductions are intentional and usually legal, though there are indications of some illegal introductions for personal aquaculture (Ruesink *et al.* 2005). Intentional introduction via aquaculture is the presumed mechanism in the majority of the rest of the Pacific oyster's global non-native range. However, research suggests that shipping may be an additional, unintentional pathway for introduction to New Zealand (Ruesink *et al.* 2005). Because oysters are benthic, encrusting organisms, hull-fouling is the likely mechanism for introductions via shipping.

Factors influencing establishment and spread

The Pacific oyster has replaced the native *O. conchaphila* as the dominant oyster species in the Pacific Northwest and has successfully established throughout the region. Pacific oysters exhibit many of the characteristics of organisms with a strong tendency toward invasion, including a close association with human activity and rapid growth.

A close association with humans is the primary factor in the global spread of *C. gigas*. Globally, most shellfish aquaculture is of Pacific oyster (Ruesink *et al.* 2005). Pacific oyster also dominates the industry in Washington State: almost 90% of all shellfish grown in Washington is *C. gigas* (PCSGA 2005). Pacific oysters are favored for commercial growth because they are hardy and grow rapidly, so it is likely that concerted efforts to introduce and spread this species will continue.

One reason that *C. gigas* dominates aquaculture production is its rapid growth. It grows up to five times faster than other oyster species (Ruesink *et al.* 2005), a trait that is highly desirable for aquaculture production and also highly undesirable in introduced species. *C. gigas* also reaches a much larger maximum size than native oysters and can grow in a wider range of temperatures and exposures (Fig 2, Ruesink *et al.* 2006). Native oysters had already declined in Washington when *C. gigas* was first introduced, and populations have not subsequently recovered, which suggests that introduced oysters may be responsible for restricting recovery of native populations. However, native oyster populations on the East coast of the U.S. have also declined and not recovered, but *C. gigas* has not successful established there. Therefore, *C. gigas* may not be actively preventing the recovery of native species; rather, introduced oysters may be filling an ecological niche left vacant by the decline of native species.

After oysters were established in Pacific northwest aquaculture facilities, they likely experienced secondary spread via both natural and human-mediated vectors. Natural spread is primarily due to escapement of adults and larvae from aquaculture farms (Dumbauld *et al*. 2008, Mills and Padilla 2004) because oysters have a 20-30 day planktonic larval phase that can lead to dispersal over long distances (Ruesink *et al.* 2005, Schmidt *et al.* 2008). Pacific oysters have high population growth rates and can spread rapidly across coastal and estuarine systems. For example, in a rapidly expanding *C. gigas* population along a 120-mile stretch of coastline in Germany, oyster abundances increased by factors of 5 to 9 over a three-year period (Schmidt *et al.* 2008). Because Pacific oysters experience high growth rates and can grow in a variety of coastal environments, this type of population growth can be expected in other coastal regions.

Oysters may also experience secondary spread via human-mediated vectors. *C. gigas* is a valuable food source and requires minimal labor or capital inputs to farm. Several shellfish growers in the Puget Sound region offer oyster seed to the general public for private shellfish culture (e.g. see http://www.taylorshellfishfarms.com/seedsales/), and Washington Sea Grant promotes “small-scale oyster farming for pleasure and profit” in a publicly available instructional manual (WSG 2004). Though private shellfish growers do need to obtain a permit from the Washington Department of Fish and Wildlife, this permit is primarily geared toward preventing the spread of oyster-associated disease and has no measures for preventing spread of non-native oyster species (WAC 220-77-040). Therefore, humans are likely playing a role in both the initial introduction and the secondary spread of non-native oysters.

Ecological and Economic Impacts

The presence of *C. gigas* in the Pacific Northwest has substantial benefits as well as costs. Pacific oysters make a major economic contribution to the region due to their dominant role in aquaculture, but as ecosystem engineers they also have major ecological impacts.

Economically, the hardiness and rapid growth of *C. gigas* are a major benefit for the aquaculture industry. In 2005, culture of Pacific oysters were worth almost $85 million in Washington State alone (PCSGA 2005), plus additional trickle-down economic benefits in related industries. In many regions in the state, shellfish aquaculture is the single largest employer (PCSGA 2005). Economic benefits are an important consideration in labeling a non-native species as 'invasive' or 'nuisance'; *C. gigas* is beneficial to many people in Washington and throughout the Pacific Northwest, so its introduction, spread, and establishment are frequently encouraged.

Pacific oysters are ecosystem engineers that have major physical impacts on their environments (Dumbauld *et al.* 2008). *C. gigas* grow in dense mats called oyster reefs, and when they grow in high densities they cause physical changes that impact the surrounding ecosystem (Escapa *et al.* 2004, Ruesink *et al.* 2006). Oysters are widely recognized for their ability to change areas of soft substrate, like mud and silt, into hard substrate (Ruesink *et al.* 2005). Modifying the substrate of large areas can alter hydrology, such as shifting marsh edges or channels (Ruesink *et al.* 2005). However, oyster reefs are hard substrates with high vertical relief, making them good environments for settlement of larval and mature benthic organisms. Several studies of oyster beds in different locations have found higher densities of benthic invertebrates, including crabs, bivalves, and worms, living on the hard substrate of oyster beds compared to surrounding soft substrate (Hosack 2003, Escapa *et al.* 2004, Dumbauld *et al.* 2008). In addition to changing the benthic environment, oysters are filter feeders that consume suspended plankton and organic matter. *C. gigas* has an especially high filtration rate (Ruesink *et al.* 2005), so dense *C. gigas* reefs can improve water clarity but also reduce food availability for native filter feeding species.

Biotic interactions with other species, both native and non-native, are an important factor in the overall impacts of invasive species. There are several beneficial impacts of *C. gigas* on native species (Dumbauld *et al.* 2008). Shorebirds spend more time foraging in *C. gigas* reefs, perhaps due to higher prey availability (Escapa *et al.* 2004). Dungeness crab recruits, *Cancer magister*, also prefer *C. gigas* reefs to other native habitat (Ruesink *et al.* 2005). However, *C. gigas* also has negative impacts on native species. Native clam species often live on Pacific oyster reefs, and because these same oyster reefs are a preferred habitat for Dungeness crab, native clams experience higher predation on reefs of *C. gigas* than in native habitat (Ruesink *et al.* 2005). Though there is no direct interaction between *C. gigas* and native clam species, this indirect link is an important consideration for managers. Other interactions among non-native species can lead to a positive feedback loop of invasional meltdowns (Ricciardi 2001). Spat of *C. gigas* has been observed growing on the stalks of the invasive marshgrass *Spartina alterniflora* (Escapa *et al.* 2004); if *S. alterniflora* crowds out native grasses and also provides a habitat for invasive oysters, symbiosis between the two species could further reduce native estuarine species.

Other negative ecological effects include the introduction of additional non-native organisms and diseases that hitchhike in shipments of oysters. People have known for decades that the introduction of non-native oysters includes a high risk of introducing other non-native species. In his seminal book on invasive species, Charles Elton proclaimed that "[t]he greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture" (Elton 1958). This still holds true today. Along the west coast of the U.S., approximately 50% of all marine invasive species were introduced via oyster aquaculture or oyster culture combined with some other vector such as shipping (Ruesink *et al.* 2005). Movement of oysters for aquaculture is recognized as one of the largest vectors for the transport of marine invasive species (Ruesink *et al.* 2005, Ruesink *et al.* 2006).

Shipments can be contaminated with cryptic species, such as the Manila clam *Ruditapes philippinarum* (Escapa *et al.* 2004), or with pest species, such as the shell-boring polychaete *Terebrasabella heterouncinata* (Ruesink *et al.* 2005). Manila clams are now established and commercially harvested in much of the same range as *C. gigas*, while *T. heterouncinata* had serious deleterious effects on the commercial abalone fishery in California (Ruesink *et al.* 2005). Shipments of Pacific oysters are also responsible for the introduction of marine grasses, including *S. alterniflora* and *Zostera japonica*, an invasive eelgrass. *Spartina* is listed as a noxious weed in Washington State, and *Z. japonica* competes directly with Washington's native eelgrass. Introduced diseases are another major concern in the oyster industry, because the introduction of non-native oysters can introduce associated non-native diseases or spread native diseases because of low tolerance (Ruesink *et al.* 2005). Regular shipments of hundreds and thousands of Pacific oysters have served as a significant vector for the introduction of hitchhiking pest species and diseases.

Current research and management efforts

Pacific oysters were intentionally introduced for economic purposes and play a major role in the regional economy, so any management strategies must strongly consider economic needs. The initial question is to consider whether *C. gigas* needs to be managed. Should it be considered an invasive species, or just a beneficial non-native species? *C. gigas* is not on Washington's list of Aquatic Nuisance Species (WDFW 2008), but it is included in the USGS Nonindigenous Aquatic Species database (USGS 2008). Some argue that human needs for food are important enough to introduce species that may have negative effects on native ecosystems, as long as these negative effects are carefully analyzed and contained (Gozlan 2008). It would be difficult to argue for, and almost impossible to achieve, complete eradication of *C. gigas*. Instead, management efforts could focus on better containing Pacific oysters within aquaculture facilities and minimizing impacts on native oysters and coastal ecosystems.

There is strong collaboration between scientists and the aquaculture industry. For example, a recent conference sponsored by Washington Sea Grant was focused on the state of current knowledge, research needs, and ways to improve sustainable shellfish culture (WSG 2007). Conference attendance included scientists, aquaculture industry professionals, and representatives of non-profit organizations. Current research is focused on reducing disease and mortality in *C. gigas*, other cultured shellfish, and associated native species. Much of what we know about *C. gigas* biology and population dynamics stems directly from research related to the aquaculture industry, so continued collaboration is desirable.

Two specific concerns are the risk of secondary spread from hatcheries and the introduction of diseases and other hitchhiking non-native organisms. The aquaculture industry has responded directly to these concerns and is working towards methods to mitigate impacts. For example, the development of triploid oysters prevents the production and spread of larvae, and triploid oysters also have better quality meat (Allen *et al.* 1989). Though 100% triploidy is often not achieved, it does reduce the secondary spread of *C. gigas* through natural dispersal (Ruesink *et al.* 2005). A clear way to reduce the spread of disease and hitchhiking species is to quarantine oysters. This practice is encouraged in the aquaculture industry (Ruesink *et al.* 2005), and state permits are required to transport shellfish, including *C. gigas*, to areas outside where they were grown (WAC 220-77-040). Preventing the spread of diseases and other detrimental hitchhikers is beneficial for the aquaculture industry, and it also helps to protect native species. Where ecosystem concerns align with industry concerns, we see better management of *C. gigas* as an invasive species.

It is also important to consider specific biotic associations and how management of *C. gigas* might affect native or invasive species. For example, *C. gigas* reefs provide good habitat for migratory and resident shorebirds (Escapa *et al.* 2004). Leaving some feral reefs intact might be a wise conservation decision, though it seems contradictory at first. Also, *C. gigas* reefs are often inhabited by the native and endangered eelgrass *Z. marina* (Ruesink *et al.* 2006), so any physical or chemical action to remove oyster reefs would also remove eelgrass. Some studies are examining ways to remove oysters or associated pest species with minimal impact on surrounding, intact native communities (Dumbauld *et al.* 2001). Though eradication of *C. gigas* is likely impossible and probably undesirable, the effects of this introduced species can be contained and mitigated.

Literature Cited

Allen S, Downing S, Chew K (1989) Hatchery manual for producing triploid oysters. Washington Sea Grant Program, Seattle.

Dumbauld BR, Brooks KM, Posey MH (2001). Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of Pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington. Mar Pollut Bull 42:826-44.

Dumbauld BR, Ruesink JL, Rumrill SS (2008) The ecological role of bivalve shellfish aquaculture in the estuarine environment: A review with application to oyster and clam culture in West Coast (USA) estuaries. *submitted*

Elton CS (1958) The ecology of invasions by animals and plants. University of Chicago Press, Chicago.

Escapa M et al (2004) The distribution and ecological effects of the introduced Pacific oyster *Crassostrea gigas* (Thunberg, 1793) in Northern Patagonia. J Shellfish Res 23:765-72.

Gozlan RE (2008) Introduction of non-native freshwater fish: Is it all bad? Fish and Fisheries 9:106-15.

Hosack G (2003) Effects of *Zostera marina* and *Crassostrea gigas* culture on the intertidal communities of Willapa Bay, Washington. M.S. University of Washington, Seattle.

Klinger T, Padilla D, Britton-Simmons K (2006) Two invaders achieve higher densities in reserves. Aquat Conserv: Mar Freshw Ecosyst 16:301-11.

Mills C, Padilla D (2004) Oysters -- an invasive tale in the San Juans. *in* Journal of the San Juan Islands, Friday Harbor.

NRC (2004) Nonnative oysters in the Chesapeake Bay. National Academies Press, Washington, D.C.

Ricciardi A (2001) Facilitative interactions among aquatic invaders: Is an 'invasional meltdown' occurring in the Great Lakes? Can J Fish Aq Sci 58:2513-425.

Ruesink JL et al (2006) Changes in productivity associated with four introduced species: Ecoystem transformation of a 'pristine' estuary. Mar Ecol Prog Ser 311:203-15.

Ruesink JL et al (2005) Introduction of non-native oysters: Ecosystem effects and restoration implications. Annu Rev Ecol Evol Sys 36:643-89.

Schmidt A, Wehrmann A, Dittman S (2008) Population dynamics of the invasive Pacific oyster *Crassostrea gigas* during early stages of an outbreak in the Wadden Sea (Germany). Helgol Mar Res 62:367-76.

Shamseldin AA et al (1997) Induced thermotolerance in the Pacific oyster, *Crassostrea gigas*. J Shellfish Res 16:487-91.

Shatkin G, Shumway SE, Hawes R (1997) Considerations regarding the possible introduction of the Pacific oyster (*Crassostrea gigas*) to the Gulf of Maine: A review of global experience. J Shellfish Res 16:463-77.

Washington Administrative Code 220-77-040. “Shellfish aquaculture disease control.”

Other Sources of Information

Oyster Identification

Hughes, JR. 2008. *Crassostrea gigas*, Pacific oyster. Marine Life Information Network: Biology and Sensitivity Key Information Sub-programme. Plymouth: Marine Biological Association of the United Kingdom. Available from: http://www.marlin.ac.uk/species/Crassostreagigas.htm

Shellfish Growers

Taylor Shellfish Farms (http://www.taylorshellfishfarms.com)

Penn Cove Shellfish (http://www.penncoveshellfish.com/)

Pacific Coast Shellfish Growers Association (http://pcsga.org/) and the associated research institute, Pacific Shellfish Institute (http://www.pacshell.org/)

Sea Grant

Reports, conference proceedings, and regional statistics from Washington Sea Grant: http://wsg.washington.edu/

Oyster Research and Restoration in U.S. Coastal Waters. Maryland and Virginia Sea Grant Programs, 8-9 Sept. 2003, Annapolis, MD. Proceedings available at: http://www.mdsg.umd.edu/issues/chesapeake/oysters/research/meeting

“Small-scale Oyster Farming for Pleasure and Profit in Washington.” Washington Sea Grant, 2002, Publication WSG-AS 0203.

“Oyster Stew: Celebrating 100 Years of Oyster Culture in Washington State.” Washington Sea Grant, 1999, available: http://www.wsg.washington.edu/oysterstew/oystermain.html

NW Workshop on Bivalve Aquaculture and the Environment. Washington Sea Grant, 13-14 Sept. 2007, Seattle, Washington. Proceedings available at: http://www.wsg.washington.edu/research/geoduck/shellfish_workshop.html

Expert Contacts

Jennifer Ruesink
Associate Professor
University of Washington, Department of Biology
24 Kincaid Hall
Seattle, WA 98195-1800
206-543-7095
ruesink@u.washington.edu
http://depts.washington.edu/jlrlab/

Brett Dumbauld, PhD
USDA, Agricultural Research Service
Hatfield Marine Science Center
2030 SE Marine Science Dr.
Newport, OR 97365
541-867-0191
brett.dumbauld@ars.usda.gov