Shellfish Aquaculture in Washington State

Final Report to the Washington State Legislature

December 2015

Washington Sea Grant

Shellfish Aquaculture in Washington State

Final Report to the Washington State Legislature • December 2015

This report provides the final results of Washington Sea Grant studies conducted from July 1, 2013 to November 30, 2015 on the effects of evolving shellfish aquaculture techniques and practices on Washington's marine ecosystems and economy. Funding provided by a proviso in Section 606(1) of the adopted 2013 – 2015 State Operating Budget.

Recommended citation

Washington Sea Grant (2015) Shellfish aquaculture in Washington State. Final report to the Washington State Legislature, 84 p.

This report is available online at
https://wsg.washington.edu/shellfish-aquaculture

Contact

Washington Sea Grant
3716 Brooklyn Avenue N.E.
Seattle, WA 98105-6716

206.543.6600
seagrant@u.washington.edu
wsg.washington.edu

WSG-TR 15-03

Acknowledgments

Washington Sea Grant expresses its appreciation to the many individuals who provided information and support for this report. In particular, we gratefully acknowledge funding provided by the Washington State Legislature, National Oceanic and Atmospheric Administration, and the University of Washington. We also would like to thank the many academic, state, federal, tribal, industry and other experts on shellfish aquaculture who cooperated with investigators to make this research possible.

Investigators/staff

Jonathan C.P. Reum,
Research Manager
Neil S. Banas
Wei Cheng
Penelope Dalton
Kevin Decker
Marcus Duke
Dara Farrell
Bridget E. Ferriss
Chris J. Harvey
Teri King
Kate Litle
P. Sean McDonald
Robyn Ricks
Jennifer Runyan
MaryAnn Wagner

Contents

Overview

Shellfish aquaculture is both culturally significant and economically important to Washington communities, and in many locations interest exists in expanding production. To promote and manage shellfish aquaculture in a sustainable manner, it is essential to understand the potential ecological and economic effects, both positive and negative, of evolving aquaculture practices. At the direction of the Washington State legislature in 2013, Washington Sea Grant initiated a research program to assess and develop tools and resources that could help growers, managers, and other coastal residents address a range of issues. The research program included an economic analysis, three pilot modeling studies, and an overview of spatial data approaches:

1. An economic trend analysis of Washington shellfish production and value (p. 1) details the economic contribution of shellfish aquaculture to different coastal areas in Washington and to the state. The analysis underscores the contribution of aquaculture to generating revenue in the state economy. Results from this work should help guide future development of economic studies and social science on the state aquaculture industry.
2. An ecosystem model of Central Puget Sound (p. 15) was developed to explore the potential influence of aquaculture on the environment and, alternatively, how environmental changes affect aquaculture. In this region, sufficient data are available to build a quantitative ecosystem model, which can be used to explore different management scenarios. For example, a finding from the model that aquaculture gear had stronger ecosystem impacts than the farmed geoduck themselves points to development of innovative gear and new culture techniques as a promising approach for minimizing impacts.
3. Relying on limited data, qualitative food web models of South Puget Sound and Willapa Bay (p. 35) can be used to identify whether shellfish populations or other food web members are likely to increase or decrease given a particular management or environmental scenario. The models for Willapa Bay, for instance, indicate that ocean acidification could potentially result in fewer Manila clams but more eelgrasses and phytoplankton. The models were relatively simple to build and can be easily refined using alternative scenarios.
4. An oceanographic study advances development of a high-resolution circulation model for South Puget Sound (p. 59). In a preliminary analysis, the model suggests that aquaculture may have the capacity to control phytoplankton concentrations in localized areas. The results strongly encourage further investigation of both the possible downstream effects on other consumers of phytoplankton and a possible role for aquaculture in mitigating eutrophication (which can be associated with water quality issues) in western South Puget Sound. The model also has a wide range of other potential applications and could be an important first step towards better prediction of seawater oxygen and acidity levels in South Puget Sound.
5. A framework and data assessment for spatial decision support in aquaculture (p. 71) can further the development of tools to support decisions such as where to site shellfish farms. A decision support study outlines the framework and includes an assessment of publicly available spatial data in Washington State that will likely be relevant. It provides a starting point for growers, managers, and researchers interested in developing spatial tools to weigh the potential ecological, social, and economic tradeoffs involved in farm placement.

SHELLFISH AND THE WASHINGTON ENVIRONMENT

Commercial shellfish cultivation has taken place in Washington waters since the mid-1800s and has evolved in terms of the species farmed, methods used, product markets, and acreage under cultivation. Today Washington State is the nation's leading producer of farmed clams, oysters, and mussels. The 2011 Washington Shellfish Initiative estimated that state shellfish growers directly and indirectly employ more than 3,200 people and provide an estimated total economic contribution of $270 million. Production includes hatcheries, nurseries, farms, and processing, distributing, wholesale, and retail operations. In addition to their commercial importance, shellfish are central to tribal cultures and economies and contribute to recreational opportunities and tourism.

Shellfish are an important component of marine ecosystems, and environmental changes and stressors can affect shellfish aquaculture production. For example, the Washington coast is especially vulnerable to ocean acidification (OA), a change in ocean chemistry that interferes with shell development in some marine organisms and which may potentially affect both cultured species and marine food web dynamics. Harmful algal blooms and aquatic invasive species also continue to pose serious threats to shellfish resources and seafood product safety. Meanwhile, climate change has introduced additional variability in environmental parameters like water temperature, contributing to and interacting with other changes.

Shifts in Washington's coastal environment have been coupled with growing human populations that affect coastal water quality and put additional pressure on regional shellfish resources. Approximately 65 percent of state residents live in coastal counties, and the Puget Sound region alone is expected to grow almost 35 percent, to five million people, by 2040. The complex challenges facing shellfish managers and growers have spurred interest in more comprehensive, ecosystem-based research that integrates environmental, social, economic, and institutional information.

2013-2015 SHELLFISH AQUACULTURE RESEARCH PROGRAM

Housed in the UW College of the Environment, Washington Sea Grant is a federal–university partnership that conducts research, education, and outreach to address Washington's coastal and marine issues and needs. In 2013, the Washington State Legislature directed Washington Sea Grant to conduct a two-year scientific research program specifically addressing state concerns related to shellfish aquaculture. The legislative language specified that funding be used to:

> … commission scientific research studies that examine possible negative and positive effects, including the cumulative effects and the economic contribution, of evolving shellfish aquaculture techniques and practices on Washington's economy and marine ecosystems. The research conducted for the studies is not intended to be a basis for an increase in the number of shellfish harvesting permits available and should be coordinated with any research efforts related to ocean acidification.

As a first step, Washington Sea Grant convened a series of scoping sessions with researchers and faculty from the University of Washington, Washington Ocean Acidification Center, and National Oceanic and Atmospheric Administration (NOAA). Based on the recommendations of session participants, a research team was assembled to develop a scope of work for the program. Although shellfish are cultured throughout Washington State marine waters, a decision was made to build on completed and ongoing research studies, focusing on program components that complemented those studies and had potential to leverage one another. This approach maximized use of existing scientific data and the geographic overlap among research program components. The resulting scope of work focused on three shellfish growing areas: Willapa Bay, Central Puget Sound, and South Puget Sound.

In March 2014, scientists with expertise in ecosystem function and ecology were asked to provide external peer reviews of the proposed research scope of work. The document was then revised in response to their comments and suggestions. The final scope included four research components in which a variety of modeling tools and approaches were used to study potential interactions between aquaculture and the environment: Puget Sound ecosystem and circulation models, qualitative food web analyses, and a synthesis of data relevant to aquaculture siting. A fifth component examined regional trends in the economic contribution of shellfish aquaculture and provides a foundation for future economic analyses.

Work on all program components commenced in May 2014. In August 2014, the research team held a workshop at The Evergreen State College with participants representing tribes, environmental groups, county planners, state and federal agencies, scientists, shellfish growers, and legislative staff. The workshop provided a forum for the team to present the goals of the research and initial work products, and for participants to provide feedback that informed the development of models and scenarios. In June 2015, chapter manuscripts were distributed to subject experts for external review, and revised and finalized by November 2015.

Consistent with the direction from the legislature, the research team's products and results are not intended to provide a basis for either increasing the availability of shellfish harvesting permits or restricting the extent or intensity of shellfish aquaculture in Washington waters. Several program components involved development of modeling tools and required the team to make a variety of assumptions about ecosystem properties. Considering those assumptions when examining model results, the team focused on evaluating general patterns and relative changes rather than precise numerical outputs. However, the models should prove useful for (1) identifying ecosystem species and attributes that may be sensitive to aquaculture practices; (2) evaluating how marine systems, including aquaculture, respond to environmental change; and (3) informing monitoring and research priorities. Products and results should lead to new insights into the ecosystem services provided by and the carrying capacity of shellfish aquaculture in Washington state.

PRODUCTS AND RESULTS

Patterns in the Economic Contribution of Shellfish Aquaculture

Kevin Decker

Understanding the economic contribution of shellfish aquaculture at the regional level is important for industry and policy decisions. In this analysis, cultured shellfish production and value were examined over time to assess economic trends based on an evaluation of seven geographical areas: South Puget Sound, Central Puget Sound, North Puget Sound, Hood Canal, Strait of Juan de Fuca, Grays Harbor and, Willapa Bay.

Because of differences in the species cultivated and in market price among species, the proportional contribution of weight versus value among areas can vary greatly. Overall, the analysis indicated that Pacific County is more dependent on shellfish aquaculture than any other county in the state. An analysis of revenue, expenses, profits, and state leases indicates an average of more than one dollar in profit for each pound of shellfish produced and $510 in annualized profit for each acre under production. The analysis highlights important differences in the economic contribution of shellfish aquaculture in the seven regions examined, but further work is needed, particularly with regard to consistent and accurate reporting of production and the value of the ecosystem services provided by shellfish in Washington State.

Evaluating Trophic and Non-Trophic Effects of Shellfish Aquaculture in the Central Puget Sound Food Web

Bridget Ferriss, Jonathan Reum, P Sean McDonald, Dara Farrell, Chris Harvey

Models of interactions between aquaculture and the environment are important for evaluating potential impacts of either environmental change or different management scenarios on cultivated species and the larger ecological community. If sufficient information is available, quantitative food web models like Ecopath with Ecosim (EwE) can be used. The models represent the main predator–prey relationships in a food web, but can be modified to include other types of relationships as well. For instance, farmed shellfish beds may have artificial structures that can increase or decrease densities of some species.

A recently developed EwE model of Central Puget Sound was updated to include commercial geoduck farms, and relationships representing the effect of geoduck anti-predator structures on several species were incorporated based on inferences from prior studies. The model suggests that, at a basin scale, the food web can support a substantial increase in geoduck aquaculture over current production levels, with only minor changes in the biomass of individual species. Nearly all the observed changes were due to the effects of predator exclusion devices as opposed to the effects of geoduck grazing on phytoplankton or acting as prey to other species. Within the model framework, increased geoduck culture resulted in higher biomass densities of surfperches, nearshore demersal fishes, and small crabs, and lower densities of seabirds, flatfishes, and certain invertebrates (e.g., predatory gastropods and small crustaceans). Such modeling exercises can help identify species that may be particularly sensitive to aquaculture expansion and warrant additional research and monitoring.

Qualitative Network Models in Support of Ecosystem Approaches to Aquaculture Production: Potential Applications to Management and Climate Change

Jonathan Reum, Bridget Ferriss, P Sean McDonald, Dara Farrell, Chris Harvey

Ecosystem-based approaches to managing aquaculture require understanding the potential ecological outcomes associated with expanding or changing aquaculture practices, and qualitative models can play an important role in this capacity. Qualitative models require basic information for forecasting abundance changes. When formally analyzed, the potential qualitative response of the entire community to an increase or decrease in one or more species can be predicted. Like quantitative food web models, qualitative models can help screen management actions for potentially unexpected outcomes or identify tradeoffs in species responses. And qualitative models have much lower data requirements compared with quantitative models.

Qualitative models were developed for South Puget Sound and Willapa Bay that describe relationships between the major cultivated species and the ecological community. For South Puget Sound, the analysis highlighted potential tradeoffs between species based on different management scenarios and actions. For example, under some scenarios, increased cultivation of one shellfish species may indirectly reduce abundance of another. For Willapa Bay, the potential effects of OA were examined. Several species responded consistently, both negatively (e.g., Manila clam) and positively (e.g., phytoplankton and eelgrasses), across a range of scenarios corresponding with different potential direct impacts of OA. Qualitative models can help identify species that strongly influence the response of the community as whole, highlight areas for future research, and summarize and integrate diverse information sources. With little additional effort, qualitative models could be developed for other areas of the state and tailored to address a wide range of questions.

An Oceanographic Circulation Model for South Puget Sound

Neil Banas, Wei Cheng

Shellfish production is dependent on phytoplankton supply, which in turn is strongly influenced by water circulation patterns. In addition, a host of other processes that affect shellfish production, including pollutant dispersal and the supply of wild larvae, depend principally on water circulation patterns. To help address these and other issues, researchers developed a new, high-resolution (200 meters) circulation model for South Puget Sound. The model was used to examine patterns for water exchange and residence-time.

In general, the surface waters in each of the major inlets in South Puget Sound disperse throughout the basin in only a few days, mainly toward the deep central channels and Main Basin. A map depicting the time required for cultured shellfish to reduce the standing stock of phytoplankton by 50%, given their inlet-scale densities, was estimated and compared with the map of water residence time. Preliminary results suggest that aquaculture may control phytoplankton concentrations in Henderson, Eld, Totten, Hammersley, and Case inlets, and Oakland Bay. This strongly encourages further investigation of both the possible downstream effects on other consumers of phytoplankton and a possible role for aquaculture in mitigating eutrophication (associated with water quality issues) in western South Puget Sound.

Geographic Information System Approaches and Spatial Datasets Relevant to Shellfish Aquaculture Siting in Washington State

Dara Farrell, Jonathan Reum, Bridget Ferriss, P Sean McDonald, Dara Farrell, Chris Harvey

Shellfish aquaculture is often just one of several competing uses for the coastal environment, and spatial analyses can help growers and managers identify tradeoffs between potential production at a given site and other economic, social, or ecological considerations. To assess and facilitate application of spatial approaches, investigators reviewed a framework to develop a farm siting geographic information system (GIS) decision support tool. The framework draws upon the most current peer-reviewed literature on GIS applications to shellfish farm siting. In addition, publicly available spatial datasets were identified for Washington State that may be relevant to future analyses. The datasets vary in terms of quality and spatial coverage and resolution, and are grouped under the following five themes: current aquaculture, physical, production, ecological and social. Datasets that are unavailable but that could prove useful for future spatial analyses were also noted. For instance, spatial data on areas that are currently and actively cultivated are unavailable; data on phytoplankton standing stocks and productivity are also largely absent. The framework and inventory of key datasets provide a starting point for developing a focused spatial research program and should be valuable to researchers, managers, and growers alike.

Patterns in the Economic Contribution of Shellfish Aquaculture

Kevin Decker, Washington Sea Grant

SUMMARY

Shellfish have been cultivated in Washington State for more than 160 years. While shellfish aquaculture production around the state has evolved and output increased, analyses of its economic contribution to the state have been sparse. Production output and pricing through 2013 was used to conduct a longitudinal analysis to assess the economic contribution of shellfish aquaculture to Washington State at a regional and state level. The analysis specifically focuses on seven regions: South Puget Sound, Central Puget Sound, North Puget Sound, Hood Canal, Strait of Juan de Fuca, Grays Harbor, and Willapa Bay (Figure 1). It revealed trends that are relevant for industry and policy analysis and provided additional metrics to highlight differences at the regional and county levels. For example, Pacific County's economy is more dependent on shellfish aquaculture than any other county in the state. Pricing for Pacific oyster, Manila clam, and mussels has historically been relatively stable, but geoduck prices have been much more volatile. Owing to differences in market price at the species level, there can be big differences between the proportional contributions of pounds versus value for a region. An analysis of average revenue, expenses, and profits reveals an average of $1.08 in profit for each pound of shellfish produced and $510 in profit for each acre under production (annualized). Revenue to the state from leasing tidelands for shellfish aquaculture varies from year to year based on a percentage of production, and it reached almost $1 million in 2013. Data on the value of ecosystem services provided by aquaculture continues to be limited, and additional research is needed to ensure this value is considered in the larger analysis of economic value to Washington State.

INTRODUCTION

The farming of oysters, clams, mussels, and geoduck in the cold, nutrient-rich, clean waters of the Pacific Northwest is a long-standing tradition and an important cultural and economic part of rural coastal communities. Shellfish farming has evolved over time, relying more and more on hatchery technology to produce the seed needed for cultivation. A handful of large-scale hatcheries produce seed shipped to numerous nurseries prior to outplanting. The nurseries allow vulnerable seed a chance to grow larger, giving it a better chance of survival after final planting. Shellfish growers also have adapted their practices to address a number of environmental challenges including ocean acidification, harmful algal blooms, water pollution, and nearshore habitat alterations.

Consumer preferences and markets have shifted as well, allowing shellfish producers to innovate with new species and new techniques for production. Key cultured species include the Pacific oyster (*Crassostrea gigas*), Kumamoto oyster (*Crassostrea sikamea*), Eastern oyster (*Crassostrea virginica*), Olympia oyster (*Ostrea lurida*), Manila clam (Venerupis philippinarum), geoduck (*Panopea generosa*), and mussels (*Mytilus trossulus* and *M. galloprovincialis*). Pacific oysters, once grown for mostly the shucked meat market, now are being tumbled and flipped to form deep-cupped oysters for the half shell market. The product mimics the deep cup of the highly prized Kumamoto oyster, whose seed availability is limited. Some harvested species such as littleneck (*Leukoma staminea*), eastern softshell clam (*Mya arenaria*), and horse clams (*Tresus nuttallii* and *T. capax)* are from wild stocks whose juveniles have settled on farmed beaches and are har-

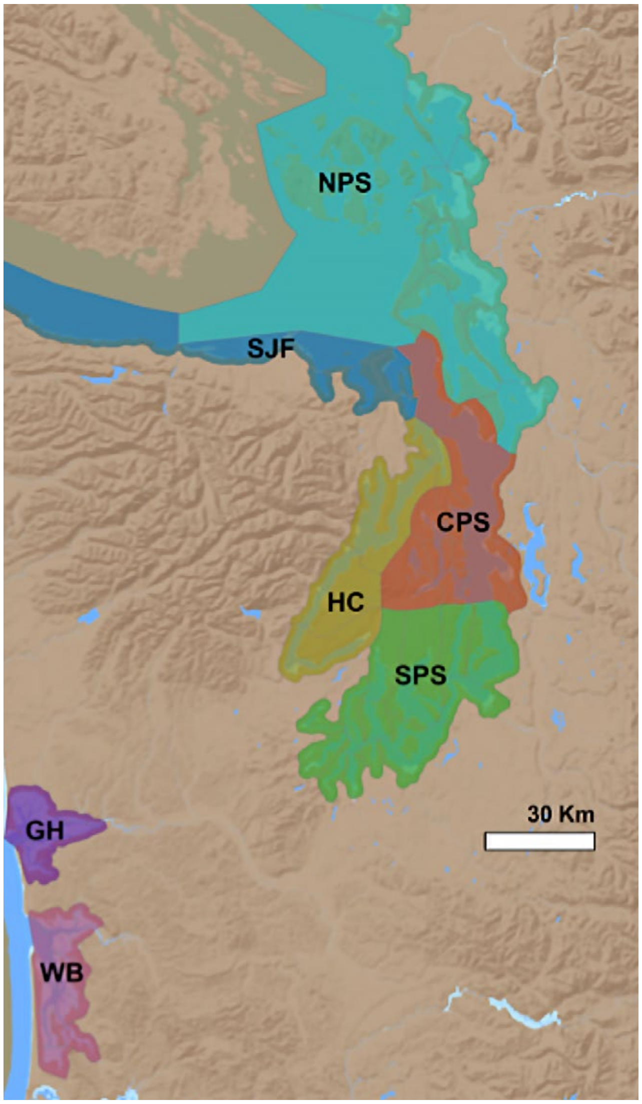


Figure 1. Map of shellfish aquaculture production regions. Delineations were based on Washington Department of Fish & Wildlife (WDFW) aquaculture area codes used for fisheries management. Production was divided into seven regions: (1) South Puget Sound, (2) Central Puget Sound, (3) North Puget Sound, (4) Hood Canal, (5) the Strait of Juan de Fuca, (6) Willapa Bay, and (7) Grays Harbor.

vested alongside cultured product. Not all tidelands are suitable for cultivating all species, so shellfish growers optimize their production farming tidelands with compatible species.

To meet the growing demand for seafood, Washington shellfish products are sold throughout the United States and exported worldwide with primary markets in Canada and Hong Kong. Currently, Washington is the leading U.S. producer of farmed bivalves with recent annual sales of nearly $150 million. Virginia is second with annual sales of $41 million, followed by Connecticut with harvests valued at $28 million (USDA 2014).

Including indirect output from industries that support aquaculture and induced output resulting from money spent in the community by aquaculture employees and supporting industries, a Northern Economics (2013) report estimated that shellfish aquaculture contributed $184 million to Washington's economy in 2010. The report also estimated the total number of jobs from shellfish aquaculture at around 1,900 and the number of indirect and induced jobs at 810. A higher number of 3,200 direct and indirect jobs was reported by the Washington Shellfish Initiative (2011). In 2010, direct aquaculture industry wages of $37 million and an additional $40 million in indirect and induced wages were paid for a Washington State total of $77 million (Northern Economics 2013).

AQUACULTURE PRODUCTION AND VALUE

To achieve a more comprehensive understanding of the economic contribution of the shellfish aquaculture industry to Washington State, it is important to understand regional differences and how the industry has changed over time. This analysis addressed these topics by evaluating regional differences in production and value using the most recent data as well as trends in historical data. It looked at production at the state level and for each of seven regions defined for this analysis (Figure 1): South Puget Sound, Central Puget Sound, North Puget Sound, Hood Canal, Strait of Juan de Fuca, Grays Harbor, and Willapa Bay. Regional delineations were based on existing aquaculture codes used by the Washington Department of Fish and Wildlife (WDFW) for fishery management. Quantity and value of shellfish aquaculture over time were examined to identify trends and a similar analysis was completed for value. The latter identified the most valuable species statewide and by region as well as changes in species value over time.

One important consideration in the analysis was the use of WDFW aquaculture production data. WFDW issues aquatic farm permits (WAC 220-69-243) and requires growers to submit accurate records showing the quantity of products sold and to provide that information quarterly. However, WDFW does not verify the production numbers submitted and there is little incentive for growers to provide accurate information to the agency. For these reasons, industry and WDFW generally consider production numbers submitted to WDFW to be underreported (B Kauffman, WDFW, personal communication). Despite this shortcoming, the WDFW data are the most comprehensive and accurate available for analysis and the only data available that have been gathered consistently over time to allow for a longitudinal analysis. All tables and figures for state and regional production and value were created from WDFW production data.

Washington State

Historical trends: Figure 2 summarizes 28 years of shellfish production data for Washington State. From 1986 until 1998, total shellfish aquaculture production stayed relatively stable, between 11.7 and 15.1 million pounds. Between 1998 and 2005, total production increased considerably, reaching a peak in 2005 at 24.9 million pounds. After 2005, production leveled off again, decreasing to a low in 2011 of 22.5 million pounds. Pacific oyster, Manila clam, and mussels have continued to be the three primary staples of shellfish aquaculture production, with the Pacific oyster maintaining the highest production by species in Washington State. Manila clam production was almost equal to Pacific oyster production in 2012, but a drop in Manila clam production in 2013 increased the gap slightly.

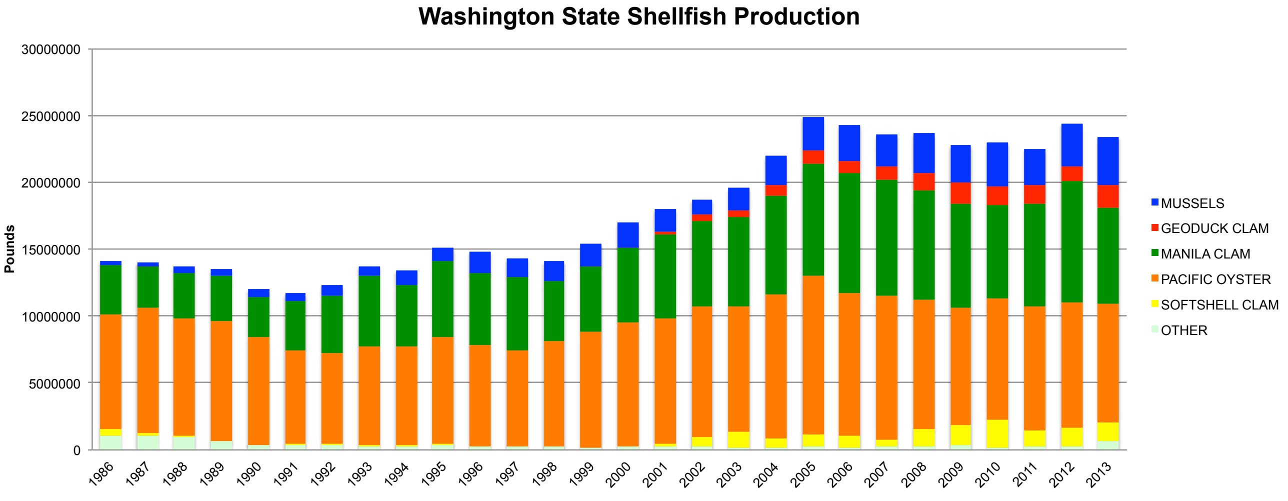


Figure 2. Washington shellfish aquaculture production by species, 1986–2013.

Current production and value: Table 1 and Figure 3 provide more detailed information on species production and value for 2013 and show that Pacific oyster accounted for 38% of total production and total value. With the expansion of the Pacific oyster market from primarily shucked meats to shucked meats and half shell, an increase in total value is expected as consumer interest in flipped and tumbled Pacific oyster takes hold. Manila clam culture accounted for 31% of production and 19% of the value. Geoduck production was previously only a very small part of total production, but it has increased substantially and now accounts for 7% of the total pounds produced and 27% of the total value for the state. In 2013, WDFW estimates for total output from shellfish aquaculture were 23.4 million pounds and $91.9 million in value.

State and regional summary: Table 2 provides summaries of production and value for 2013, indicating that South Puget Sound is the top producing region with 37% of total production and almost 58% of total value. Willapa Bay is second with 25% of production and almost 17% of the value. Species importance varies between Puget Sound and the Pacific coast, with the Sound primarily producing Manila clam and coast mainly producing Pacific oyster.

Table 1. Weight and value of Washington shellfish aquaculture production by species, 2013 (percentages are rounded to the nearest whole number for all tables).

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Mussels	3,655,551	16	7,940,408	9
Geoduck clam	1,613,114	7	24,482,209	27
Manila clam	7,259,401	31	17,451,985	19
Pacific oyster	8,793,138	38	34,853,940	38
Softshell clam	1,419,509	6	454,198	<1
Other	664,905	3	6,738,647	7
Total	23,405,618	100	91,921,390	100

Table 2. Regional summary of 2013 Washington aquaculture production and value.

	Production		Value	
Region	**Pounds**	**Percentage**	**Dollars**	**Percentage**
South Puget Sound	8,664,322	37	53,230,541	58
Central Puget Sound	5,253	<1	19,411	<1
North Puget Sound	3,926,994	17	7,311,343	8
Hood Canal	3,490,795	15	11,566,475	13
Strait of Juan de Fuca	155,467	<1	455,587	<1
Willapa Bay	5,948,216	25	15,567,786	17
Grays Harbor	1,209,895	5	3,956,918	4
Total	23,400,942	100	92,108,061	100

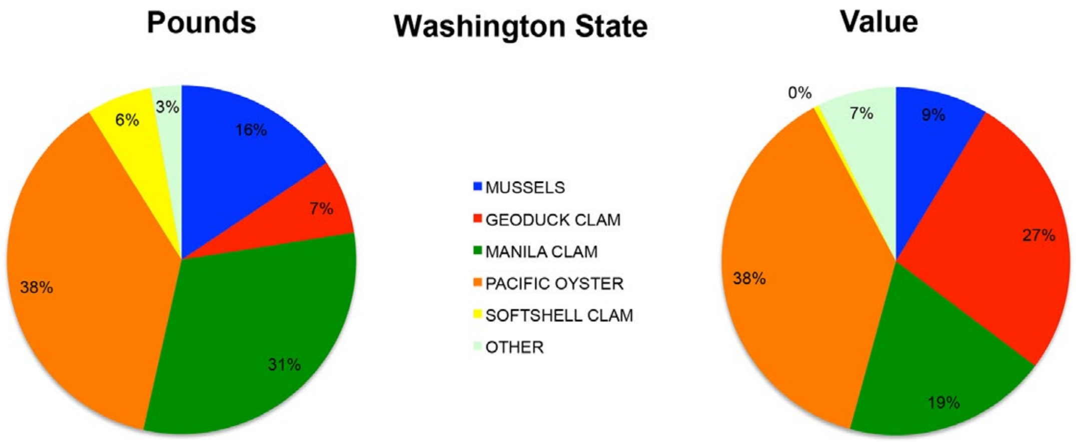


Figure 3. Percentages for 2013 harvest weight and value of Washington shellfish species.

South Puget Sound

Historical trends: As indicated in Figure 4, long-term data for South Puget Sound show the Manila clam has been the primary cultured species in terms of landings but production has decreased since peak reported landings in 2006. Until recently, Pacific oyster was the second most produced species but was surpassed by geoduck in 2010 and mussels in 2011. Geoduck production began to increase in 2000 and has maintained a mostly upward trajectory. Two native species, Olympia oyster and littleneck clam, continue to be a small part of overall landings.

Current production and value: More detailed 2013 information provided in Table 3 and Figure 5 shows that South Puget Sound has low levels of production for butter clam (*Saxidomus gigantea*), cockle (*Clinocardium nuttallii*), European flat oyster (*Ostrea edulis*), Kumamoto oyster, Eastern oyster, horse clams, littleneck clam, and Olympia oyster. Together, these species made up less than one percent of the total landings in terms of weight and value in 2013. While geoduck clams accounted for only 18% of pounds produced, they contributed 44% of the regional value. In addition to cultured product, there was a substantial wild harvest of geoduck clams in South Puget Sound. According to WDFW catch records, in 2013 the wild geoduck harvest totaled 479,739 pounds, valued at $3.6 million. Wild harvest from all Washington Department of Natural Resources (WDNR) geoduck tracts are strictly managed and a tract is left fallow for many years during natural tract recovery. Manila clam had the highest production by weight (42%) of production, but only accounted for 16% of total value.

Table 3. Weight and value of South Puget Sound production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Mussels	1,767,688	20	4,615,502	9
Eastern oyster	140,628	2	1,953,601	4
Geoduck clam	1,573,169	18	23,648,591	44
Kumamoto oyster	118,826	1	2,901,719	5
Manila clam	3,654,315	42	8,546,063	16
Pacific oyster	1,342,967	15	11,472,384	22
Other	66,729	<1	92,678	<1
Total	8,664,322	100	53,230,541	100

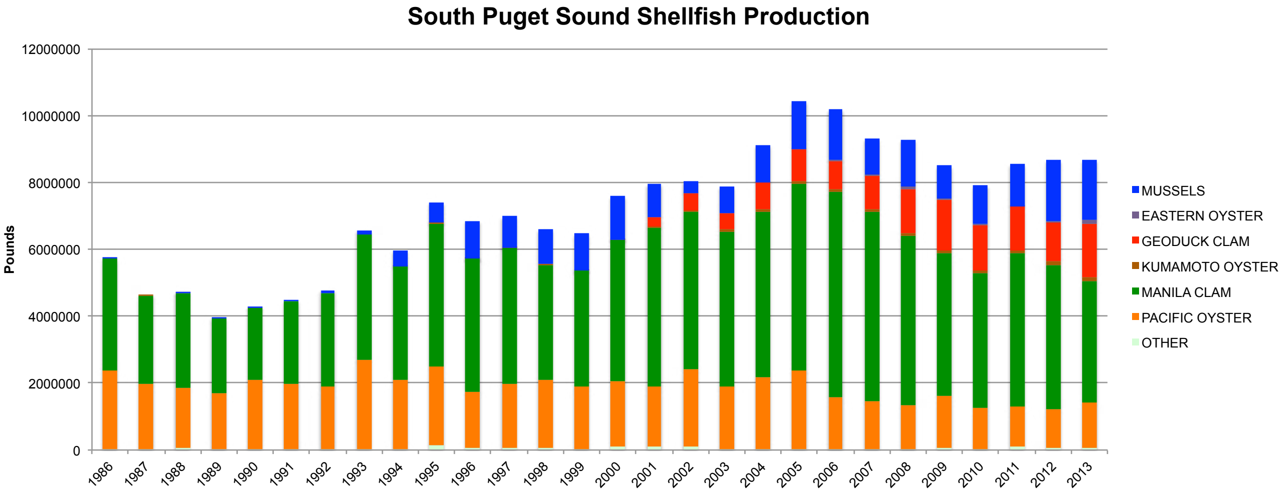


Figure 4. South Puget Sound shellfish aquaculture production by species, 1986–2013.

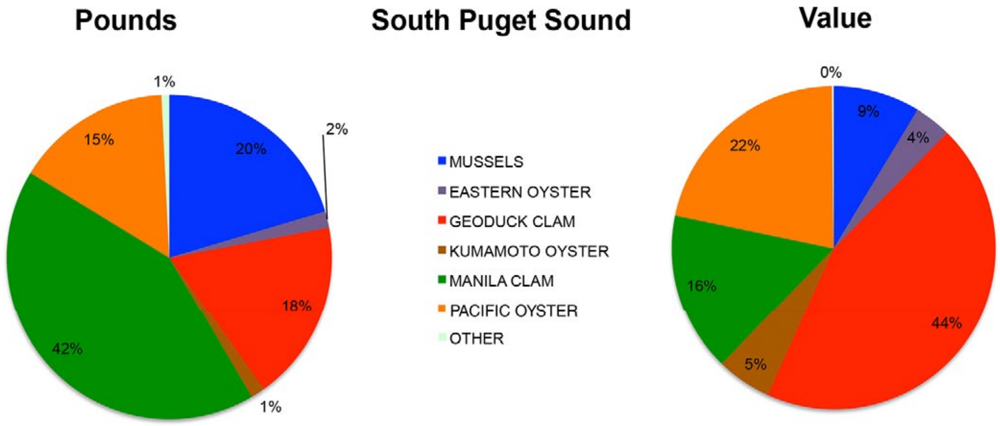


Figure 5. Percentages for 2013 harvest weight and value of South Puget Sound shellfish species.

Central Puget Sound

Historical trends: As shown in Figure 6, Central Puget Sound produced primarily Pacific oyster between 1986 and 1995. Production reached a peak of just over 560 thousand pounds in 1989 and dropped precipitously in 1995. Since 1995, only very small amounts of shellfish aquaculture have been attributed to Central Puget Sound as that region is defined for this analysis.

Current production and value: As shown in Table 4 and Figure 7, Central Puget Sound is currently producing just two species: Manila clam, which accounts for 87% of production and 64% of value; and Pacific oyster, which accounts for the remaining 13% of production and 36% of value. The 2013 production of all species in the region accounted for less than one percent of state production and value.

Table 4. Weight and value of Central Puget Sound production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Manila clam	4,570	87	12,339	64
Pacific oyster	683	13	7,072	36
Total	5,253	100	19,411	100

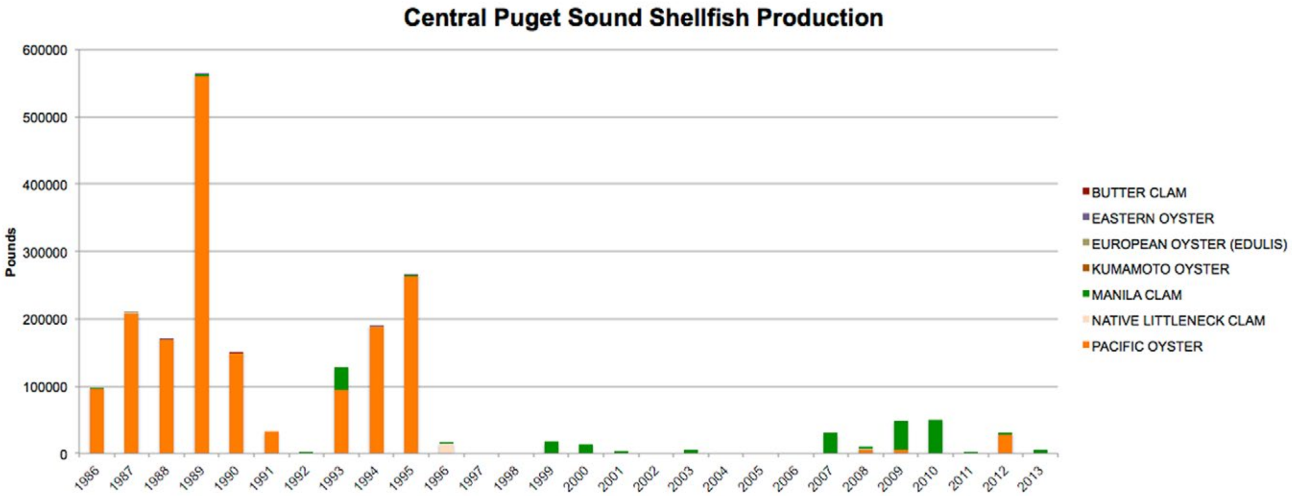


Figure 6. Central Puget Sound shellfish aquaculture production by species, 1986–2013.

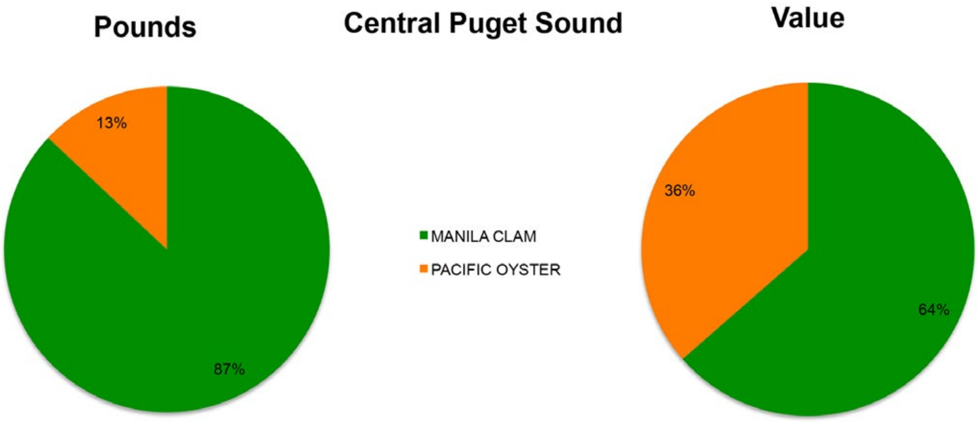


Figure 7. Percentages for 2013 harvest weight and value of Central Puget Sound shellfish species.

North Puget Sound

Historical trends: As Figure 8 summarizes, North Puget Sound primarily lands mussels and softshell and Manila clams. The region saw consistent growth in cultured mussels from 1998 until 2010, followed by a dramatic decrease in 2011. Dropping from 1.8 million pounds in 2010 to 447 thousand pounds in 2011, mussels rebounded back to 1.47 million pounds by 2013. Softshell clams peaked in 2010, with production of 2.1 million pounds, dropped to 920 thousand by 2012, and bounced back slightly to 1.4 million pounds by 2013.

Current production and value: As Table 5 and Figure 9 show, in 2013 mussels topped North Puget Sound production in terms of weight and value. Softshell clams contributed 36% of the harvest but only 6% of the value, while Pacific oyster culture accounted for only 6% of production but 23% of the value.

Table 5. Weight and value of North Puget Sound production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Mussel	1,473,464	38	2,497,982	34
Eastern oyster	56,356	1	413,231	6
Manila clam	751,062	19	2,063,479	28
Pacific oyster	226,404	6	1,688,582	23
Softshell clam	1,419,304	36	454,146	6
Other	404	<1	193,920	3
Total	3,926,994	100	7,311,343	100

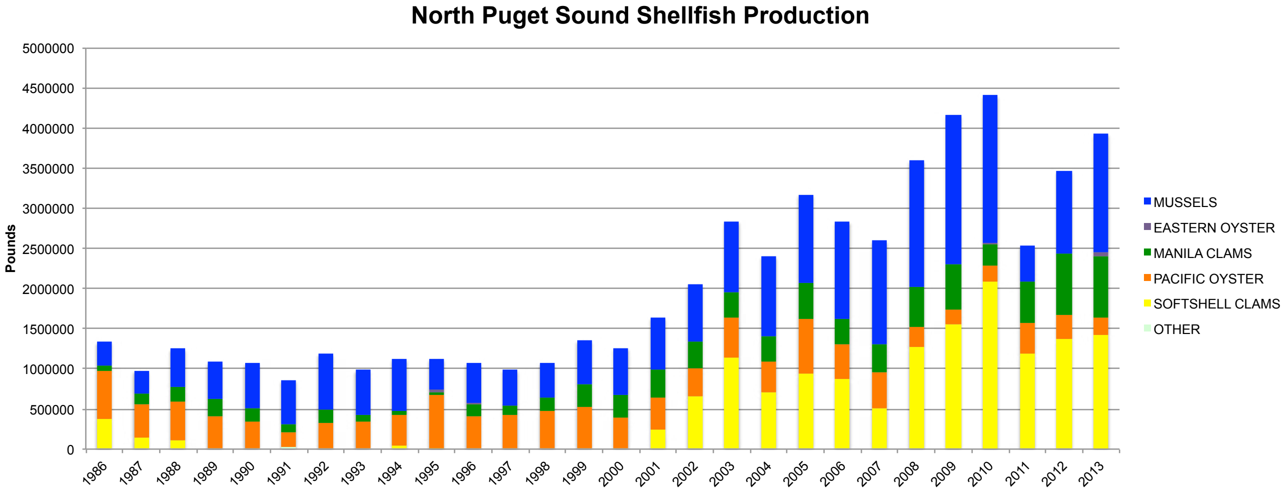


Figure 8. North Puget Sound shellfish aquaculture production by species, 1986–2013.

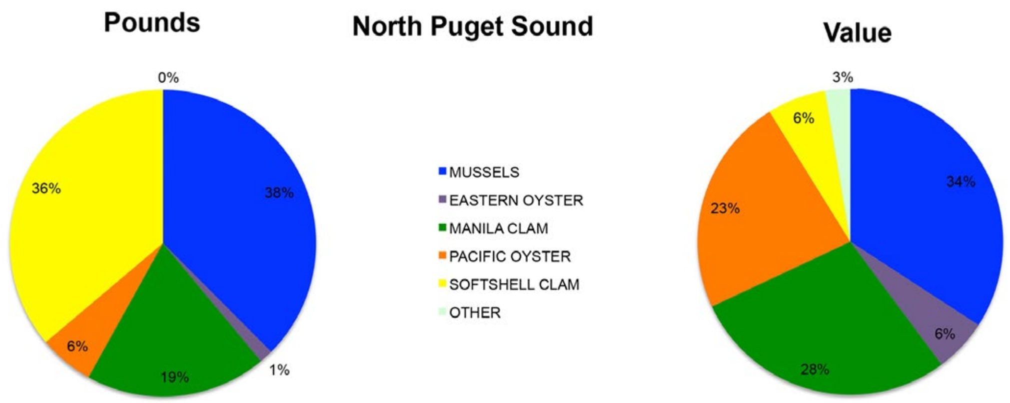


Figure 9. Percentages for 2013 harvest weight and value of North Puget Sound shellfish species.

Hood Canal

Historical trends: As indicated by Figure 10, Manila clam and Pacific oyster have been the staple species of shellfish aquaculture in Hood Canal since 1989. In 2010, a mussel culture operation expanded into the region and mussels have continued to be important for the region since then. Native littleneck clams were harvested in large numbers between 1986 and 1988, at which point production dropped from 389 thousand pounds to just under 4 thousand pounds in 1989. Manila clams have seen the steadiest growth in production over time, experiencing 41% growth during the last 10 years. In 2013, Pacific oyster production increased significantly from 711 thousand pounds to 1.3 million pounds.

Current production and value: Because of the growth in Pacific oyster production, the species accounted for 39% of total 2013 production and 46% of the year's value as shown in Table 6 and Figure 11. The Manila clam continued to be the primary species by weight, accounting for 47% of regional production and 40% of the value. Mussels accounted for 12% of production and 7% of value. While geoduck contributed less than one percent of production, its high prices accounted for 6% of the total value.

Table 6. Weight and value of Hood Canal production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Mussels	414,000	12	826,027	7
Geoduck clam	29,212	<1	639,698	6
Manila clam	1,657,173	47	4,674,670	40
Pacific oyster	1,344,865	39	5,311,618	46
Other	45,545	1	114,461	<1
Total	3,490,795	100	11,566,475	100

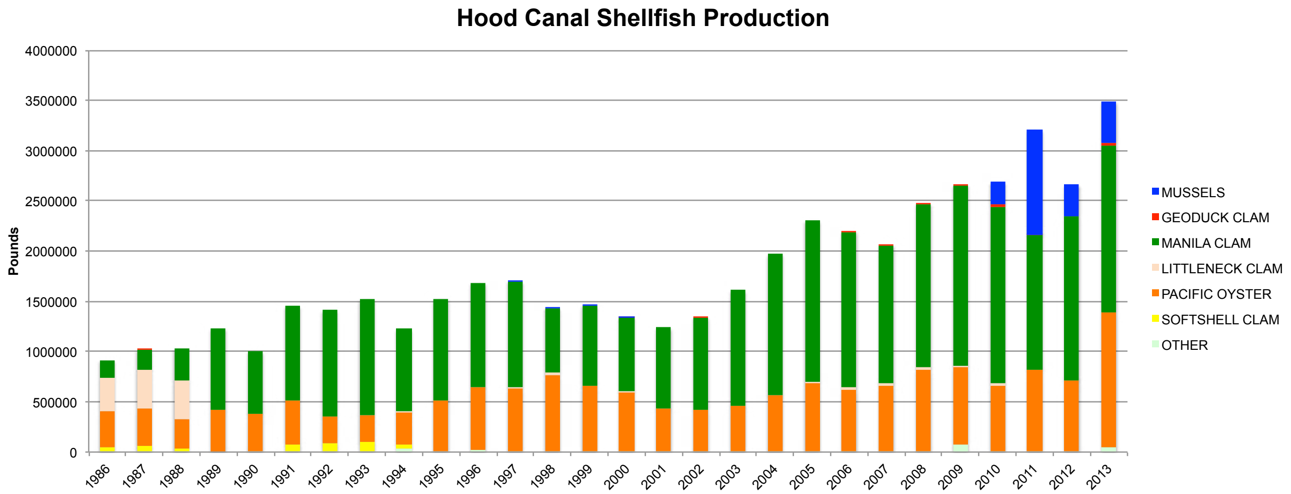


Figure 10. Hood Canal shellfish aquaculture production by species, 1986–2013.

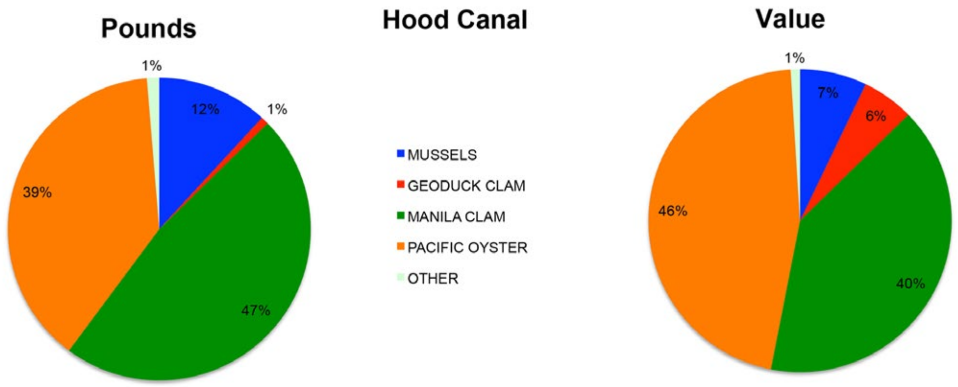


Figure 11. Percentages for 2013 harvest weight and value of Hood Canal shellfish species.

Strait of Juan de Fuca

Historical trends: As indicated in Figure 12, the Strait of Juan de Fuca saw a substantial decrease in production between 1986 and 2013, from more than 743 thousand pounds down to 155 thousand pounds. In 1986, the native littleneck clam was the primary species harvested, but it became less of the proportional mix over time. Butter clam, geoduck, Manila clam, and Pacific oyster have also been important species for the region. Geoduck production first started in the region in 2006 and has continued at a low level since then, with no production in 2008

Current production and value: The more detailed 2013 information provided for the Strait in Table 7 and Figure 13 confirms a total harvest of 155 thousand pounds. While geoduck accounted for less than 7% of total production, it accounted half the value for the region. Because WDFW provided no value for the region's geoduck production, value was extracted based on the average price per pound for Hood Canal during this same period. Butter clams accounted for 21% of harvest but less than one percent of the value for the region.

Table 7. Weight and value of Strait of Juan de Fuca production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Butter clam	32,791	21	9,542	2
Geoduck clam	10,329	7	226,205	50
Manila clam	54,163	35	96,435	21
Littleneck clam	20,737	13	21,438	5
Pacific oyster	31,610	20	99,836	22
Other	5,837	4	2,128	<1
Total	155,467	100	455,587	100

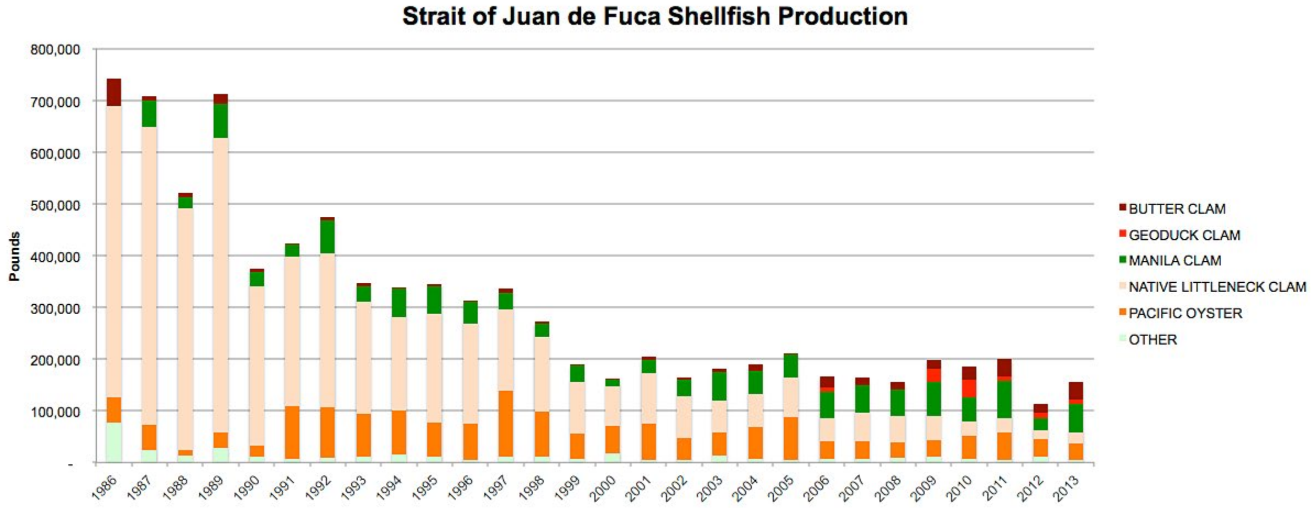


Figure 12. Strait of Juan de Fuca shellfish aquaculture production by species, 1986–2013.

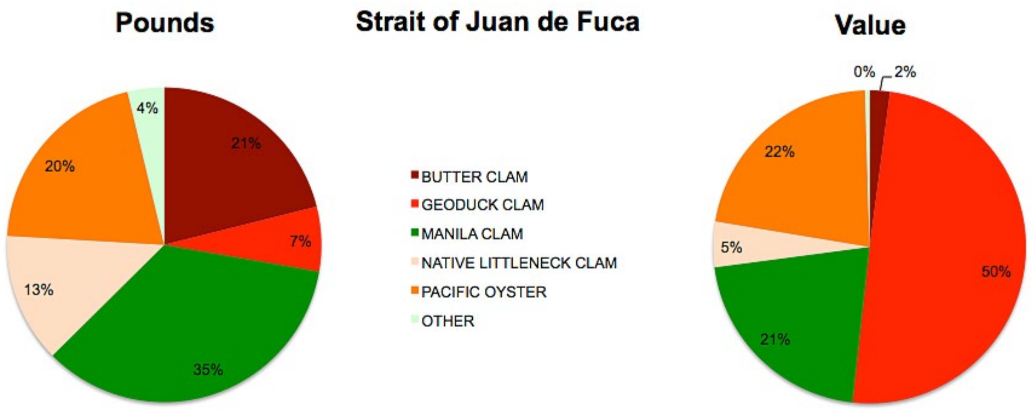


Figure 13. Percentages for 2013 harvest weight and value of Strait of Juan de Fuca shellfish species.

Willapa Bay

Historical trends: Figure 14 shows Willapa Bay production for two primary species, Manila clam and Pacific oyster. Manila clam production appears to have leveled off between 1.1 and 1.2 million pounds. Pacific oyster production has been a little more variable: it peaked in 2007 with 7 million pounds produced and $15.8 million in value. Since 2008, production has gone up and down in alternating years.

Current production and value: As Table 8 and Figure 15 demonstrate, in 2013 Willapa Bay production was dominated by Pacific oyster and Manila clam, accounting for 78% and 19% of total production, respectively. Mussels and Kumamoto oysters were negligible contributors to overall production, but the Eastern oyster accounted for almost 3% of production and 8% of the value.

Table 8. Weight and value of Willapa Bay production by species, 2013.

	Weight		Value	
Species	**Pounds**	**Percentage**	**Dollars**	**Percentage**
Eastern oyster	177,451	3	1,229,106	8
Manila clam	1,135,168	19	2,051,032	13
Pacific oyster	4,635,525	78	12,286,434	79
Other	72	0	1,211	<1
Total	5,948,216	100	15,567,786	100

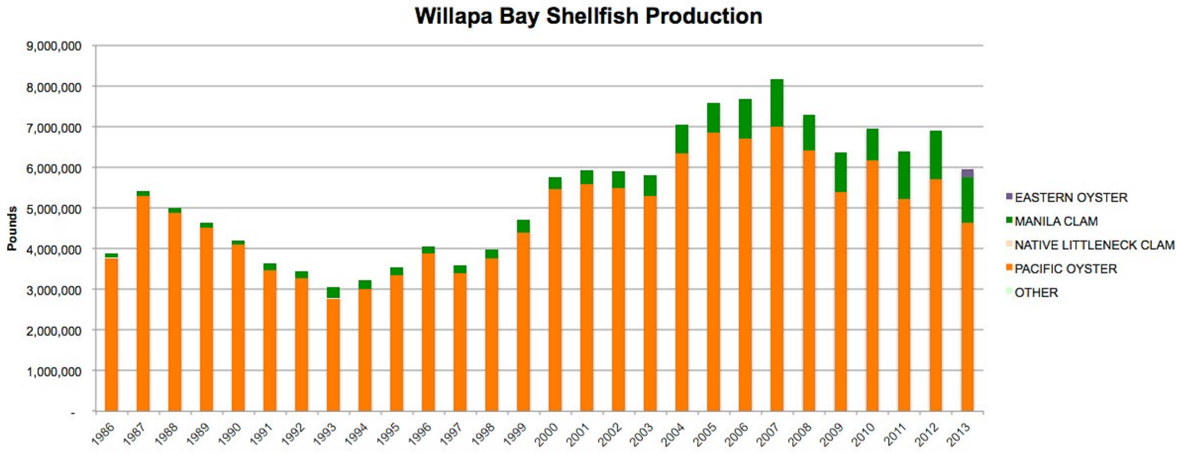


Figure 14. Willapa Bay shellfish aquaculture production by species, 1986–2013.

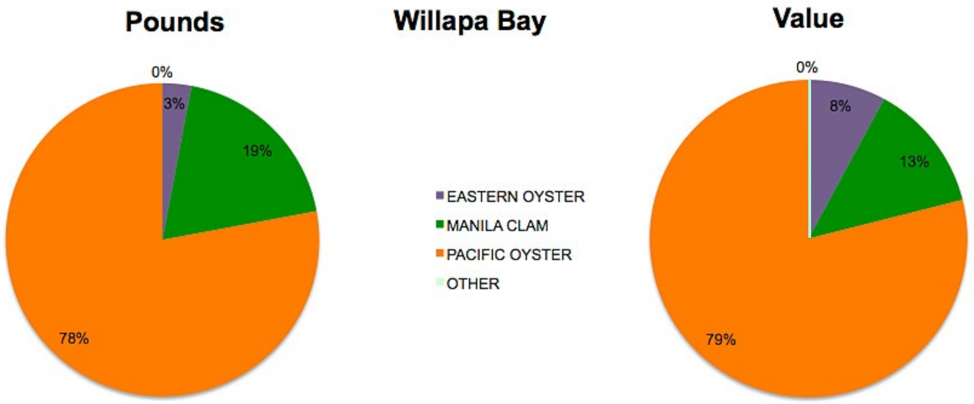


Figure 15. Percentages for 2013 weight and value of Willapa Bay shellfish species.

Grays Harbor

Historical trends: As shown in Figure 16, Grays Harbor production relied almost exclusively on the Pacific oyster, with small amounts of cockles harvested between 1994 and 1997 and Manila clam cultivated in 2004, 2012, and 2013. In 2011, Pacific oyster harvests increased to an all-time high of 1.6 million pounds with a value of $5.3 million.

Current production and value: Total Grays Harbor production in 2013 was 1.2 million pounds valued at $3.9 million. Manila clam contributed less than one percent by weight and value to total production (Table 9).

Table 9. Weight and value of Grays Harbor production by species, 2013.

	Weight		Value	
Species	Pounds	Percentage	Dollars	Percentage
Manila clam	2,950	<1	7,965	<1
Pacific oyster	1,206,945	>99	3,948,953	>99
Total	1,209,895	100	3,956,918	100

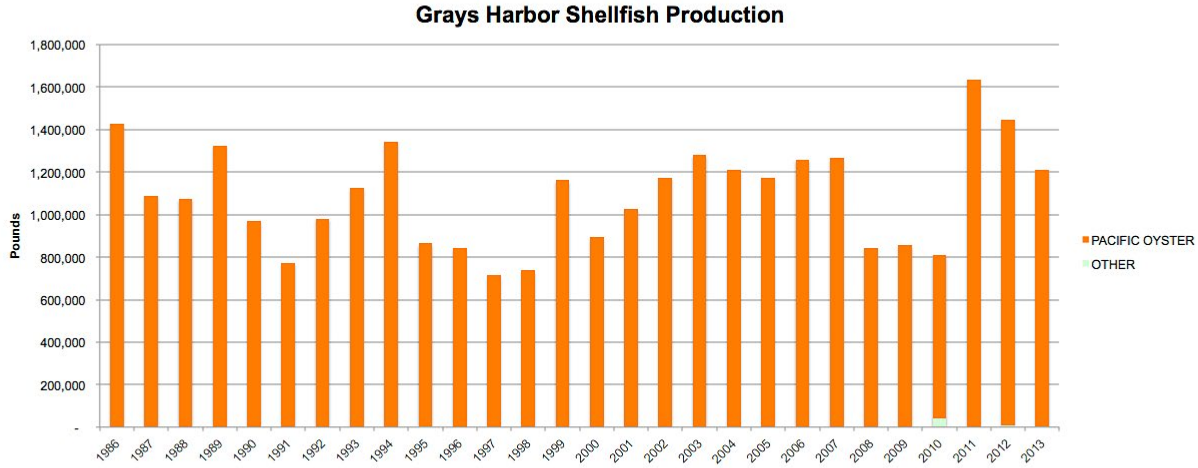


Figure 16. Grays Harbor shellfish aquaculture production by species, 1986–2013.

OTHER ECONOMIC CONSIDERATIONS

Contribution to Regional Economies

Shellfish aquaculture is important, particularly in rural counties, because it helps to diversify local economies and provides jobs. Estimates of economic contribution reflect the proportional contribution of shellfish aquaculture relative to the whole economy at county or state levels. While this value demonstrates the importance of an industry, it also highlights potential economic risk if the industry reduces business activities, relocates, or closes down.

The contribution of shellfish aquaculture to a county's economy was calculated using the 2010 gross domestic product (National Ocean Economics Program 2015) and county-level aquaculture output from the Northern Economics (2013) report. Combining information from the two data sources facilitated determination of the proportional contribution of shellfish aquaculture to each county. Results indicated that Pacific County was the most aquaculture-dependent county in the state with almost 20% of its economy relying on aquaculture. By contrast, the contribution in other counties and for Washington as a whole was less than five percent. While this value seems quite small, it reflects the complexity and size of the overall economy upon which counties and the state rely.

Price Stability

Evaluating the price for shellfish aquaculture species over time helps to assess its stability or volatility. All prices were derived from WDFW production and value numbers and converted to 2013 dollars. Prices for the primary species produced in Washington are provided in Figures 17, 18, and 19. Figure 17 shows that mussels and Pacific oyster have had relatively stable prices. Although Eastern and Kumamoto oyster prices have been more volatile, they provided a higher price per pound. Prices for Kumamoto oysters have been particularly variable, experiencing jumps in 2006 and 2008, then dropping in 2010 to stabilize around $23 per pound. In 2013, Eastern oysters experienced a slight drop in price.

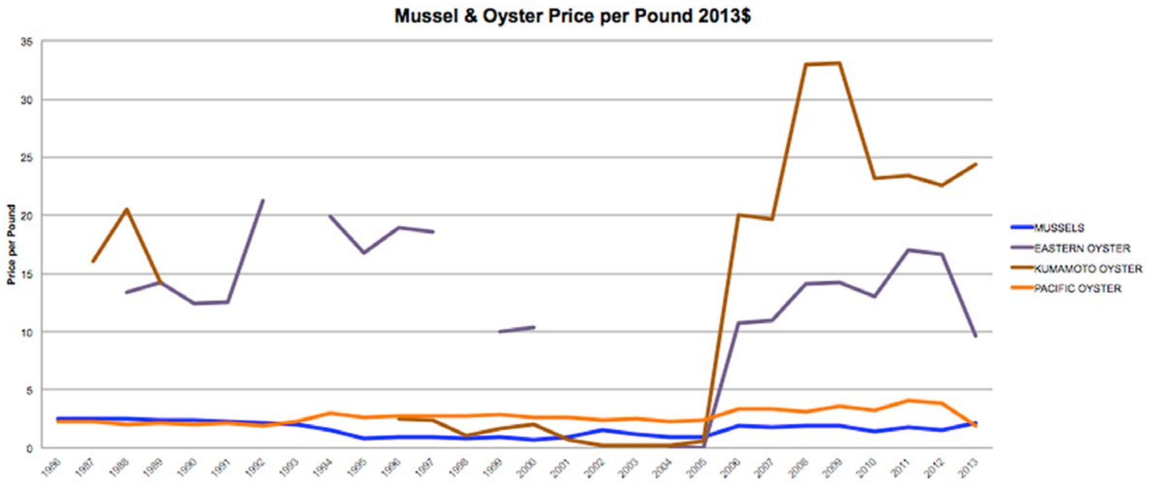


Figure 17. Average price in 2013 dollars for mussels and oysters in Washington, 1986–2013.

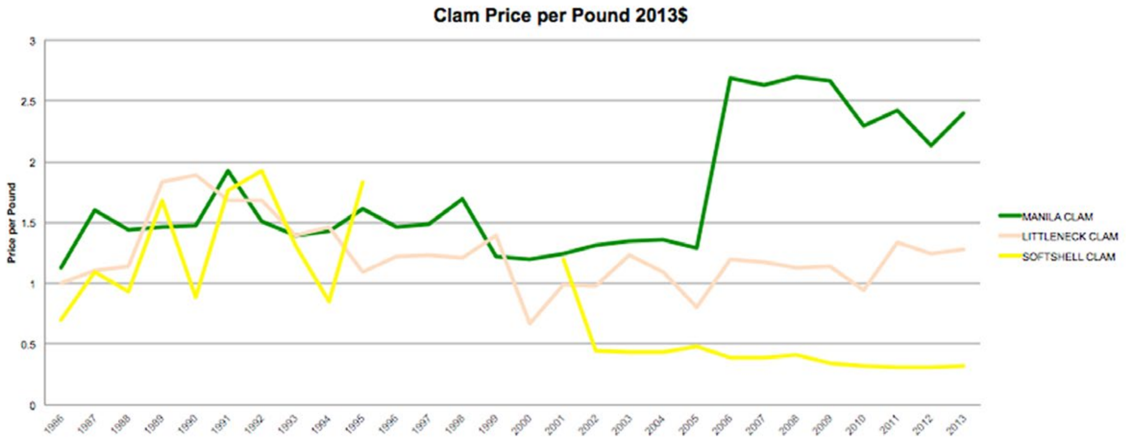


Figure 18. Average price in 2013 dollars for clams in Washington, 1986–2013.

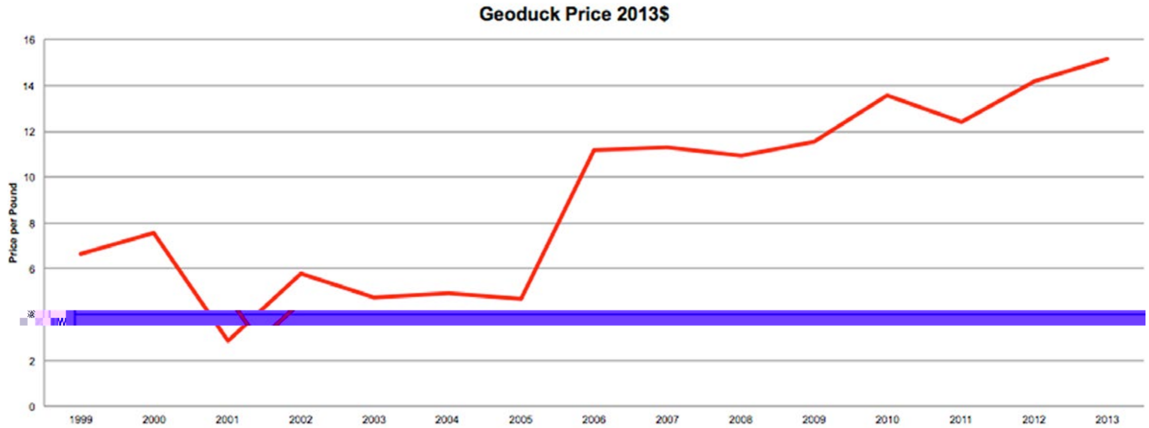


Figure 19. Average price in 2013 dollars for geoduck in Washington, 1999–2013.

Manila, littleneck, and softshell clams had similar pricing through the 1990s but began to diverge in the early 2000s (Figure 18). Now, there are relatively large price differences between them, with Manila providing the highest price, followed by littleneck and softshell. The price of littleneck clams has been relatively stable over time. The Manila clam has experienced a doubling in price — $1.29 in 2005 to $2.69 in 2006 — and has maintained prices around that level ever since. Softshell clam experienced high volatility and intermittent pricing until 2002, where prices stabilized between $0.31 and $0.48 (Figure 18) and a robust commercial fishery took hold. Geoduck has a significantly higher price than any of the other species being produced in large quantities, and pricing for geoduck appears to be continuing its upward trajectory (Figure 19).

Price stability for each species was evaluated by calculating the coefficient of variation (CV) of price, a unit-less measure that facilitates direct comparison between species over time (Table 10). A higher CV indicates a higher level of volatility in the price. Because the CV is unit-less, a doubling of the value indicates that the price is twice as volatile. The price difference was calculated by subtracting the average price during 2004–2008 from the average price during 2009–2013 using 2013 real prices. These two recent 5-year averages were used to provide price smoothing and to demonstrate the long-term pricing trend.

Overall, pricing volatility decreased between the two time periods, indicating that prices have been stabilizing. Kumamoto oysters had the highest price volatility between 2004 and 2008, and cockles between 2009 and 2013.

Industry Contribution

On average, the shellfish aquaculture industry generates $4.75 in revenue, $3.67 in expenses, and $1.08 in profit for every pound of shellfish produced (Table 11). Comparatively, for every acre under production, there is $5,497 in revenue, $4,987 in expenses, and $510 in profit (Table 11). The values are statewide averages, aggregated owing to data limitations. They may vary widely for an individual firm based on the species produced, production method, location, firm size, and level of vertical integration. These factors could substantially affect the individual firm's revenue, profit, and expenses, and wide variation in these values would be expected.

Tideland Lease Revenue

The WDNR leases state tidelands for the production of shellfish aquaculture. Lease amounts are based on a percentage of production and fluctuate from year to year. Lease revenue data include subtidal and intertidal leases but do not include physical structures — such as docks, moorings, or piers — or WDFW leases. Lease revenue information provided in Table 12 was obtained from WDNR's lease management system, NaturE. Pacific and Grays Harbor counties have 1,622 acres under lease that produce an average rental fee of $93 per acre. The Puget Sound region has fewer acres under agreement, but generates more lease revenue: The average in Puget Sound is about $1,900 per acre, twenty times more than Pacific and Grays Harbor counties. An estimated 2,288 acres are in production in Grays Harbor County and 17,288 acres in Pacific County, for a total 19,576 acres (Northern Economics 2013). This indicates that approximately 8% of farmed acreage in Pacific and Grays Harbor counties is leased from the state, and the remaining acreage is privately owned or leased. Puget Sound has an estimated 10,085 acres under production, 436 of which are leased from the state. This translates to about 4% of the tidelands in Puget Sound being leased from WDNR for shellfish aquaculture. The two coastal counties also have more total agreements and more acres covered in each agreement. In Washington State, an estimated 7% of shellfish production takes place on tidelands leased from WDNR.

Table 13 provides five years of data on state revenue generated by tideland leases for shellfish aquaculture. In 2010, WDNR received more than $1 million in lease revenue, but the amount dropped the subsequent year to less than half that sum. By 2014, revenue regained a level that was nearly equivalent to revenue generated in 2010.

Table 10. Average price per pound for each species and coefficient of variation (CV) for 2004–2008 and 2009–2013, and average price per pound difference between the two time periods. All prices in dollars. Created from WDFW production data.

Species	2004–2008 Average Price	2004–2008 CV	2009–2013 Average Price	2009–2013 CV	Average Price Difference
Mussels	1.50	0.36	1.75	0.17	0.25
Butter clam	0.60	0.23	0.52	0.53	-0.08
Cockle clam	0.25	0.03	0.59	0.59	0.34
Eastern oyster	7.18	0.93	14.12	0.21	6.94
Geoduck clam	8.60	0.40	13.37	0.11	4.76
Kumamoto oyster	14.71	0.96	25.35	0.17	10.64
Manila clam	2.13	0.35	2.38	0.08	0.25
Littleneck clam	1.08	0.15	1.19	0.13	0.11
Olympia oyster	70.15	0.53	131.64	0.25	61.49
Pacific oyster	2.89	0.19	3.33	0.26	0.43
Softshell clam	0.42	0.09	0.32	0.04	-0.10
Total	2.68	0.28	3.25	0.10	0.57

Table 11. Revenue, expenses, and profit for the shellfish aquaculture industry based on per pound and per acre units. Created from Northern Economics (2013).

	Dollars per Pound	Dollars per Acre
Revenue	4.75	5,497
Expenses	3.67	4,987
Profit/Income	1.08	510
Total	24.4 million pounds	18,450 farmed acres

Table 12. Statewide, Pacific and Grays Harbor counties, and Puget Sound aquaculture lease information. Source: Washington Department of Natural Resources (WDNR).

	Pacific and Grays Harbor Counties	Puget Sound	Statewide
WDNR Lease revenue	$150,781	$828,511	$979,292
Acres under lease	1622	436	2,058
Total leases	70	51	121
Average acres/lease	23	9	17
Revenue/acre	$93	$1,900	$476

Table 13. Statewide tidelands lease revenue, 2010–2014.

Year	Statewide WDNR tideland lease revenue for shellfish aquaculture
2014	$979,292
2013	$644,870
2012	$645,147
2011	$505,334
2010	$1,023,567

Ecosystem Services

Ecosystem services are the benefits provided to people from nature (Millennium Ecosystem Assessment 2005). Owing to the difficulty in valuing ecosystem services, many of them are frequently not considered when assessing economic value or contribution, and this may result in underestimation of the overall importance of these services. Shellfish, for example, play a key role in coastal ecosystems, contributing multiple services and providing value beyond their market price. While it is important for Washington State to recognize the economic value provided by ecosystem services from shellfish, limited work has been done and more is needed.

In general, ecosystem services can be separated into the four broad categories of provisioning, regulating, habitat or supporting, and cultural (Millenium Ecosystem Assessment 2005). Key ecosystem services that may be provided by shellfish include the following (adapted from Brumbaugh and Toropova 2008):

- Provisioning — subsistence and commercial fisheries, aquaculture, fertilizer and building materials, and jewelry and other decoration
- Regulating — protection of coastlines from storm surges and waves, water quality maintenance, reduction of shoreline erosion, and stabilization of submerged land by trapping sediments
- Habitat or supporting — nursery habitats and cycling of nutrients
- Cultural — tourism and recreation, and as a symbol of coastal heritage

Provisioning services are ecosystem services that describe the material or energy outputs from ecosystems. For shellfish, food and habitat provisioning are among the most widely cited services (Soto et al. 2008) and the economic value of food in particular is relatively easy to measure. However, remaining categories of ecosystem services are much more difficult to measure and remain largely unquantified for shellfish in Washington State.

Regulating services are those that act as regulators of other variables or processes in the ecosystem. For instance, as filter feeders, bivalves remove particulates including phytoplankton from the water column, which can help combat symptoms of eutrophication that primarily result from excessive nitrogen loading in coastal waters. In Oakland Bay, nitrogen removal through shellfish harvest amounted to 11.7 metric tons per year, or 0.87% of the total nitrogen loading from all sources (Steinberg and Hampden 2009). In Puget Sound, nitrogen removal by bivalves was 62 metric tons per year, or 0.04% of the total nitrogen load (Steinberg and Hampden 2009). Estimated value of the benefits to water quality from nitrogen removal ranged from $25,300 to $815,400 (2007 dollars) in Oakland Bay (Burke 2009) based on a replacement cost methodology. Similar methods could be used to extrapolate the economic value of nitrogen removal across the state. Changes to the costs of existing technology or the development of new technology could dramatically change the value of shellfish for nitrogen removal.

Shellfish aquaculture can also provide structured habitat, which can benefit species of commercial or conservation value. A single square meter of oyster reef may provide as much as 50 square meters of surface area, which provides attachment points and shelter for various plants and animals (Bahr and Lanier 1981). Oyster reefs attract a variety of species, resulting in complex interactions; these reefs are considered essential fish habitat (Coen et al. 1999).

Cultural ecosystem services are nonmaterial benefits people obtain from ecosystems through spiritual enrichment, cognitive development, reflection, recreation, and aesthetic experiences, as well as the identity and sense of place of an area provided by the ecosystem. Cultural ecosystem services from shellfish in Washington State can be seen in South Bend, which is known as the "Oyster Capital of the World," and Oysterville, which was named because of the rich oyster beds of Willapa Bay. These cities are symbolic of the region's heritage. Cultural ecosystem services are difficult to characterize and especially difficult to measure with an economic value (Chan et al. 2012, Donatuto and Poe 2015). This difficulty often results in their omission from decision making. Regardless of the framework used, it is important to include cultural services when assessing the economic contribution of shellfish to Washington State.

CONCLUSION

Washington State continues to be a national leader in shellfish aquaculture, and the industry continues to grow and innovate. The shellfish aquaculture industry is an important element of the overall Washington State economy. The industry provides needed revenues and jobs to the coastal economies of which it is a part; for example, it contributes as much as 20% of the total economy for Pacific County. Each region has a unique mix of species and the industry contributes varying levels of economic value to each region. Based on the geographic delineations used in this report, South Puget Sound generates more production and value than any other region: 37% of total harvest weight and almost 58% of the industry's value. Manila clam, Pacific oyster, and mussels continue to be important species for the entire Puget Sound, but geoduck is becoming more important to the region. Willapa Bay relies primarily on the production of Pacific oyster and Manila clam, and Grays Harbor relies almost exclusively on Pacific oyster. The Puget Sound region, particularly South Puget Sound, is increasing its reliance on geoduck, which introduces additional risk and price volatility to those growers in the region. Grays Harbor and Willapa Bay's reliance on Pacific oyster and Manila clam provides a level of stability to these regions, since the pricing for these species tends to be much less volatile.

Shellfish aquaculture is a profitable industry and can provide economic opportunities for those seeking entry. While future expenses are difficult to predict, pricing seems relatively consistent, adding some stability to the revenue side of the industry. Washington benefits from the taxes on revenue and jobs generated by the industry and also from revenue paid directly to the state to lease tidelands for production. Puget Sound generates substantially more lease revenue than other regions — more than five times the revenue of Grays Harbor and Willapa Bay combined. Since revenues are based on a percentage of production, a growing shellfish aquaculture industry means growing lease revenues for the state. In addition to the more explicit monetary contributions from the industry, ecosystem services should be considered in any analysis that seeks to evaluate the economic contribution of shellfish aquaculture.

In order to accurately assess the economic contribution of shellfish aquaculture to Washington State, an ongoing, accurate, and consistent data-gathering process is needed. Future research should address data limitations, the primary barrier to comprehensive and accurate representation of the industry. Additionally, production of shellfish does not exist in isolation. There are additional economic benefits from shellfish aquaculture created from secondary products and services such as shucking and packing houses, transport, manufacturing of prepared oyster products, and retail sales (Northern Economics 2013). These benefits are not captured in this report, and additional research into their economic contribution to Washington State would provide a more comprehensive picture of the contribution of the overall industry than that provided by only production. There is also a substantial knowledge gap in assessing the economic value of the ecosystem services provided by shellfish aquaculture. It is important to understand if these services differ from the services provided by natural stock and restored sites, as well as the effects of these services on value. Future research should focus on identifying and quantifying the value of ecosystem services and assessing changes.

LITERATURE CITED

Bahr LM, Lanier WP (1981) The ecology of intertidal oyster reefs of the South Atlantic coast: a community profile. FWS/OBS-81/15, US Fish and Wildlife Service, Washington, DC, 105 p.

Brumbaugh RD, Toropova C (2008) Economic valuation of ecosystem services: a new impetus for shellfish restoration. Basins and Coasts News 2(2):8–15.

Burke S (2009) Estimating water quality benefits from shellfish harvesting; a case study in Oakland Bay, Washington. Technical memorandum, Entrix, Seattle, 15 p.

Chan KM, Satterfield T, Goldstein J (2012) Rethinking ecosystem services to better address and navigate cultural values. Ecological Economics 74:8–18.

Coen LD, Luckenbach MW, Breitburg DL (1999) The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. In Benaka LR (ed), Fish Habitat: Essential Fish Habitat and Rehabilitiation. American Fisheries Society Symposium 22, Bethesda, Maryland, pp. 438–454.

Donatuto J, Poe MR (2015) Evaluating sense of place as a domain of human well-being for Puget Sound restoration. Final report to Puget Sound Institute, 80 p.

Millennium Ecosystem Assessment (2005). Millennium ecosystem assessment: ecosystems and human well-being (Vol. 5). Island Press Washington, DC.

National Ocean Economics Program (accessed February 19, 2015) Coastal economy data by county. Available at *http://www.oceaneconomics.org/Market/coastal/coastalEcon.asp.*

Northern Economics (2013) The economic impacts of shellfish aquaculture in Washington, Oregon and California. Bellingham, WA, 33 p. plus appendix.

Soto D, Aguilar-Manjarrez J, Hishamunda N. (2008) Building an ecosystem approach to aquaculture. In FAO/Universitat de les Illes Balears Expert Workshop, Palma de Mallorca, Spain, May 7–11, 2007, 7 p. plus annexes.

Steinberg P, Hampden J, (2009) Nitrogen removal with shellfish harvest in Oakland Bay and Puget Sound. Technical Memorandum prepared for The Pacific Shellfish Institute, p. 16.

USDA (United States Department of Agriculture) (2013). Census of Aquaculture (Volume 3, Special Studies, Part 2 No. AC-12-SS-2) (p. 98).

Washington Shellfish Initiative (2011) Puget Sound Partnership, Olympia, WA.

Evaluating Trophic and Non-Trophic Effects of Shellfish Aquaculture in the Central Puget Sound Food Web

Bridget Ferriss, Jonathan Reum, Washington Sea Grant; P Sean McDonald, University of Washington (UW) School of Aquatic and Fishery Sciences; Dara Farrell, UW Department of Mechanical Engineering; Chris J Harvey, NOAA Fisheries, Northwest Fisheries Science Center, Conservation Biology Division

ABSTRACT

Expansion of the shellfish aquaculture industry may affect the structure and dynamics of coastal estuarine food webs. To better understand potential food web tradeoffs, trophic and non-trophic interactions (e.g., habitat facilitation, predator refuge) were incorporated into a food web model of Central Puget Sound to predict the potential effects of an increase in geoduck (*Panopea generosa*) aquaculture. At a basin scale, the food web can support at least a 120% increase in geoduck aquaculture over current production levels (based on landings of 10,546 kilograms in 2012), with only minor changes in individual species' biomass or metrics of ecosystem resilience. The non-trophic effects of increased geoduck aquaculture, related to the influence of anti-predator structure, had a stronger influence on the food web than the trophic role of cultured geoducks as filter feeders and prey to other species. Increased geoduck culture caused substantial increases in biomass densities of surf perches, nearshore demersal fishes, and small crabs, and decreases in seabirds, flatfishes, and certain invertebrates (e.g., predatory gastropods and small crustaceans). This study identifies species that should be a priority for additional empirical research and monitoring related to bivalve aquaculture interactions, including demersal fishes, small crustaceans, and seabirds. It also provides insights into the benefits and challenges of incorporating habitat-related data into a food web model. Understanding these relationships can inform management decisions by clarifying tradeoffs in ecosystem functions and services in Puget Sound, and can facilitate estimation of direct and cumulative effects of bivalve aquaculture at a food web scale.

INTRODUCTION

Bivalve aquaculture is a rapidly growing, global industry that occurs primarily in coastal waters and depends upon functioning, productive ecosystems. Interactions between cultured bivalves and the environment can vary with species, growout method, harvest and maintenance disturbance regimes, and development scale (Dumbauld et al. 2009, Simenstad and Fresh 1995). In regions with high bivalve densities and water retention times, bivalves may locally deplete phytoplankton (Asmus and Asmus 1991, Banas et al. 2007), potentially reducing symptoms of eutrophication (Zhou et al. 2006). However, bivalve aquaculture may also alter the composition of benthic communities (Cheney et al. 2012, Dubois et al. 2007, Dumbauld et al. 2009, Simenstad and Fresh 1995) and influence the abundance and distribution of higher trophic level animals such as seabirds (Connolly and Colwell 2005, Faulkner 2013, Zydelis et al. 2009). Understanding these potential interactions is important to sustainably manage industry expansion and is critical for supporting ecosystem-based management approaches to aquaculture development (Cranford et al. 2012, NRC 2010).

Food web models, such as Ecopath with Ecosim (EwE; Christensen and Walters 2004, Polovina 1984), are useful tools for addressing resource management issues in an ecosystem context. To date, applications of EwE to bivalve aquaculture have been restricted to modeling the trophic relationships of bivalves as filter feeders and prey to other species (Byron et al. 2011a, Jiang and Gibbs 2005, Leloup et al. 2008). However, bivalve aquaculture may also have important non-trophic effects. Changes in pelagic–benthic coupling, competition for space, prey concentration, predator refuge, and altered habitat structure (either biogenic structure or gear structure) may change the behavior of species and influence interspecific interactions (see review by Dumbauld et al. 2009; NRC 2010). The potential non-trophic effects of aquaculture are widely documented but are often difficult to incorporate into traditional food web models.

Mediation functions are a tool within Ecosim that simulate the influence of a third (mediating) variable on predator–prey interactions, following Wootton's (1994) definition of an interaction modification. Mediation functions can be used to describe non-trophic interactions between species or between species and habitats within a food web modeling framework (Ainsworth et al. 2008, Espinosa-Romero et al. 2011, Ma et al. 2010, Plummer et al. 2013). For example, mediation functions can be applied to systems in which shellfish farms modify the vulnerability of prey to predators through facilitation (e.g., concentrating prey, thereby increasing predation) or protection (e.g., refuge that decreases predation). The mediation effect is the enhancement or dampening caused by the shellfish farm on predator–prey interactions (Christensen et al. 2000). Widespread use of mediation functions is limited by the dearth of knowledge of their functional shape and the strength of the mediating relationships (Harvey 2014), and they typically require regionally specific, empirical data to paramaterize. McDonald et al.'s (2015) study on the interaction of geoduck aquaculture and the surrounding community provides the data needed to overcome these limitations.

Presently, geoduck (*Panopea generosa*) is the most valuable shellfish cultivated in intertidal Washington State. Recent reported landings have approached 589,670 kilograms with an estimated value of $18,500,000 (2010 aquaculture landings estimates, Washington Department of Fish & Wildlife [WDFW]). As suspension feeders, geoducks have a direct trophic effect on phytoplankton, but non-trophic effects resulting from the cultivation process may also influence community members (McDonald et al. 2012, McDonald et al. 2015, Price et al. 2012). Geoduck aquaculture production occurs on a five- to seven-year cycle. In the early phase of the cycle, a common practice is to protect newly outplanted juvenile geoduck (i.e., seed) from predators by placing them inside vertically oriented sections of polyvinyl chloride (PVC) tube (10-15 centimeters diameter) inserted into the tideflat; the tubes are then covered with netting to eliminate predator access (McDonald et al. 2015). Initial stocking density is typically 20-30 clams per square meter (VanBlaricom et al. 2015). These anti-predator structures are removed after approximately two years, once the clams have reached a size and depth that minimize most predation (McDonald et al. 2015). Market-sized geoducks are eventually harvested individually by hand in the sixth or seventh year in a process of liquefaction whereby a harvester uses a hose to inject large volumes of low-pressure water into sediments around the clam to loosen and extract it (VanBlaricom et al. 2015). In Puget Sound, Washington, McDonald et al. (2015) and VanBlaricom et al. (2015) showed that anti-predator structure and disturbance resulting from harvest of cultured geoducks, respectively, can suppress some benthic species while promoting others; thus, culture practices likely have important mediation effects. Empirical data from such studies can help evaluate the effects of geoduck aquaculture expansion on the food web and assess the relative importance of trophic versus non-trophic interactions on the community in a single modeling framework.

This study revised and expanded a previously published EwE model of the Central Puget Sound (Harvey et al. 2012a) to help evaluate the potential ecological effects of geoduck aquaculture expansion. Central Puget Sound is the largest of four subbasins that compose Puget Sound, a major fjordal system located in Washington State (Figure 1). Currently, Central Puget Sound supports significantly less geoduck harvest relative to other major shellfish-producing regions in Washington State, but the potential to develop geoduck culture further exists. In this study, investigators examined the potential effects of geoduck aquaculture on the Central Puget Sound ecosystem. Specific goals were to (1) explore the potential influence of trophic and non-trophic interactions on biomass predictions in a food web model and (2) identify potential community and ecosystem responses to increased geoduck farming. First an existing, dynamic, mass-balanced food web model of Central Puget Sound was modified to include cultured shellfish functional groups and mediation functions were added that captured the non-trophic effects of geoduck culture on the surrounding food web. Subsequently, the potential trophic and non-trophic effects of expanded geoduck aquaculture on community structure were calculated under varying scenarios of expansion.

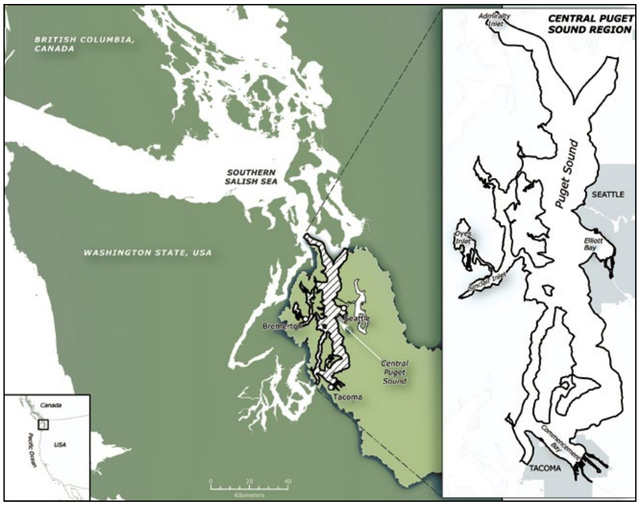


Figure 1. Map of Central Puget Sound, the spatial domain for the Ecopath with Ecosim (EwE) model, and the rest of the southern Salish Sea, as well as catchment areas (lightly shaded) that feed directly into Central Puget Sound. Inset shows Puget Sound in more detail (Harvey et al. 2012a).

MATERIALS AND METHODS

Model Development

A recently parameterized EwE model of Central Puget Sound (Harvey et al. 2012a) was modified to incorporate ecological relationships between geoduck aquaculture and the larger food web. The Central Puget Sound model domain drains a total area of 35,500 km^2, encompassing all marine habitat between the Tacoma Narrows (47.2681°N, 122.5506°W) in the south to Whidbey Island (47.9013°N, -122.3778°W) in the north (Figure 1). Central Puget Sound includes intertidal habitats dominated by sand, gravel, and occasional eelgrass or algal habitats and mud-bottomed subtidal habitats that exceed depths of 250 m in some areas (Figure 1). In addition, the region includes large bays and numerous pocket estuaries, and it receives freshwater inputs from moderately sized rivers (Cedar, White, and Green rivers).

As a general overview, investigators first revised the EwE model to include additional taxonomic detail regarding nearshore biota relevant to intertidal bivalve aquaculture. Next, they incorporated mediation functions into the model that corresponded to the non-trophic effects of geoduck culture on other species. The functions were directly informed by field experiments and observations (McDonald et al. 2015) and corresponded to mediation effects that reduced the vulnerability of certain species to predation (i.e., predator refuge) or increased the search rate of predators (i.e., habitat exclusion). Last, investigators ran scenarios in Ecosim simulating increased geoduck aquaculture.

The Ecopath model (Christensen and Pauly 1992, Polovina 1984) balances biomass gains and losses for each functional group using the following expression:

$$B_i \cdot \left(\frac{P}{B}\right)_i \cdot EE_i = BA_i + Y_i + \sum_{j=1}^{n} B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} \qquad \text{Equation (1)}$$

where the biomass (B), production to biomass ratio (P/B) and ecotrophic efficiency (EE) (the fraction of production used in the system) of prey group *i* are balanced with the biomass accumulation (*BA*) and mortalities due to fisheries (*Y*) of prey group (*i*), and predation by all groups *j*. Predation mortality is calculated using the biomass of all predator groups *j*, the consumption to biomass ratio (*Q/B*) of all predator groups, and the fraction of group *i* in the diet of each group *j* (*DC*). Ecopath uses matrix inversion to calculate one parameter (often *B* or *EE*) for each group based on inputs of the other parameters such as diet, production, consumption, and mortality rates.

Ecosim adds a temporal dynamic to the food web model, allowing biomass of functional groups to change based on trophic dynamics, harvest, other mortality, immigration, and emigration. A set of differential equations are solved in Ecosim based on the following form:

$$\frac{dB_i}{dt} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \qquad \text{Equation (2)}$$

where $dB_i \cdot dt^{-1}$ represents the growth rate of group *i*. Biomass increases with net growth efficiency (g_i), total consumption of group *i* (Q_{ji}), and immigration (I_i). Biomass decreases with predation mortality (Q_{ij}) by all predators on group *i*, non-predation mortality (M_i), fishing mortality (F_i), and emigration (e_i).

The Central Puget Sound model was revised to include additional detail in nearshore functional groups and cultured geoduck groups (Table 1 and Appendix tables 1–3, p. 27). Specifically, migratory shorebirds (e.g., dunlins, great blue herons), small brachyuran crabs, and red rock crab were added. Also, the existing infaunal bivalve group was divided into two groups: large- and small-bodied bivalves. Large-bodied bivalves consisted principally of species of interest to recreational and commercial harvesters (e.g., butter clam, horse clam, heart cockle). Small-bodied bivalves included those not targeted by commercial or recreational harvest (e.g., purple *Transennella* and amethyst gem clam).

Cultured geoducks were added as a multistanza group to separate the stages in which anti-predator structure is present (years 1 to 2), anti-predator structure is absent (years 3 to 5), and harvest occurs (years 6 to 7). The Central Puget Sound standing stock biomass was calculated based on the 2012 aquaculture landings estimate of 10,546 kilograms (WDFW) and an average geoduck weight of 0.7 kilograms at harvest. Estimated natural mortality rate is 50% from outplanting to harvest, with half the mortality occurring in the first 2 years (B Phipps, Taylor Shellfish, J Gibbons, Seattle Shellfish, personal communication). The von Bertalanffy growth equation was used to calculate individual growth (maximum length = 158 millimeters, length at maturity = 75 millimeters, k = 0.19; Bradbury and Tagart 2000, Calderon-Aguilera et al. 2010), and logistic growth was used to estimate number of geoducks over time. von Bertalanffy growth was used to keep consistent with the Ecopath biomass calculations for multi-stanza groups. Density (metric tons per square kilometer (t km^{-2})) was determined by dividing these biomass estimates by the product of total area in Central Puget Sound (757.08 square kilometers (km^2); Harvey 2012a) and proportion of that area in the 0- to 10-meter depth range (0.14 km^2; Harvey 2012a). The resulting densities are 5.3 t km^{-2} (year 1-2), 9.7 t km^{-2} (year 3-5), and 5.03 t km^{-2} (year 6-7). The density would be largely underestimated in planted areas and overestimated in unplanted areas. This is consistent with how other Ecopath population densities are estimated.

Mediation

Ecosim mediation functions can simulate the influence of a functional group or species on the strength of predator–prey interactions between a different pair of species. The consumption rate (*Q*) of prey (*i*) by predator (*j*) is defined in Ecosim as follows:

$$Q = \left(\frac{a_{ij}}{A_{ij}}\right) \cdot \frac{v_{ij} \cdot B_i}{\left(2V_{ij} + \frac{a_{ij}}{A_{ij}} \cdot P_j\right)} \cdot P_j \qquad \text{Equation (3)}$$

where a_{ij} is the rate of effective search for *i* by *j*, A_{ij} is the search area in which *j* forages for *i*, v_{ij} is the flow rate of biomass (B_i) between pools that are vulnerable or invulnerable to predation, and P_j is the abundance of *j* in A_{ij}. A mediation function influences a_{ij}, A_{ij}, and (or) v_{ij} according to a user-defined function. An increased v_{ij} makes *i* subject to greater top-down control and increasing a_{ij} makes *j* a more efficient consumer of *i*. Input mediation multipliers range from zero to one and are rescaled by Ecosim to equal one when the biomass of the mediating group is at its initial baseline density.

Investigators included two sets of mediation functions: non-aquaculture related interactions previously published for the Central Puget Sound model (Harvey et al. 2012b, Harvey 2014, Plummer et al. 2013), and those based on an empirical study of the effects of geoduck culture on macrobenthic communities in South Puget Sound (Table 1; McDonald et al. 2015). Following Plummer et al. (2013), increasing eelgrass biomass was allowed to positively mediate v_{ij} values for the prey of juvenile salmon (i.e., greater top-down control as eelgrass aggregates prey); negatively mediate v_{ij} values for juvenile salmon and young of the year crab (i.e., more bottom-up control as eelgrass increases and provides refuge from nearshore predators); and positively mediate the a_{ij} value for juvenile Pacific herring (greater juvenile herring productivity as eelgrass increases and provides spawning substrate). Harvey et al. (2012a) described a behavioral mediation effect where resident and overwintering bald eagles (the mediating groups) harass nearshore diving and herbivorous seabirds, which causes them to expend more energy to avoid eagle predation while foraging. That is, the variables A_{ij} (of the nearshore diving and herbivorous seabirds) and v_{ij} (of their prey), which relate foraging ability, were modeled as a decreasing function of increasing eagle biomass.

The geoduck aquaculture mediation functions are primarily based on observed numerical responses of benthic invertebrates to anti-predator structure (partially buried PVC tubes with net covers) placed on plots with outplanted geoducks over their first two years (Table 1). Functional groups thought to gain refuge from the anti-predator structure, and that exhibited higher biomass densities inside geoduck plots with anti-predator structure, had mediation functions wherein vulnerability to

Table 1. Mediation effects specific to geoduck culture in Puget Sound (McDonald et al. 2015) and added to the central Puget Sound EwE model. Sign (+ or -) in the EwE Group column indicates the effect of geoduck culture on the functional group, as observed by McDonald et al. (2015). The superscript numbers 1 and 3 associated with the mediation parameter indicate whether the mediation function is based on the effect of anti-predation structure in the first stanza of culture (years 1 and 2) or due to harvest disturbance in the third stanza (years 6 or 7). Mediation parameters correspond to an increase (+) or decrease (-) in the vulnerability (v_{ij}) of the prey ($_i$) or search rate ($_{aij}$) on the predator ($_j$).

Species/group *(McDonald et al. 2015)*	**EwE group**	**Mediation parameter**
Starry flounder (*Platichthys stellatus*) Sand sole (*Psettichthys melanostictus*)	Small mouth flatfishes (-)	$-\alpha_{\text{surf perch, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{shrimp, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{YOY crab, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{other grazers, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{small crabs, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{small mouth flatfishes, barnacles}}^{(1)}$ $-\alpha_{\text{soft infauna, small mouth flatfishes}}^{(1)}$ $-\alpha_{\text{deposite feeders, small mouth flatfishes}}^{(1)}$
Speckled sanddab (*Citharichthys stigmaeus*)	Piscivorous flatfishes (-)	$-\alpha_{\text{surf perch, piscivorous flatfishes}}^{(1)}$ $-\alpha_{\text{demersal fishes, piscivorous flatfishes}}^{(1)}$ $-\alpha_{\text{shrimp, piscivorous flatfishes}}^{(1)}$ $-\alpha_{\text{other grazers, piscivorous flatfishes}}^{(1)}$ $-\alpha_{\text{small crabs, piscivorous flatfishes}}^{(1)}$ $-\alpha_{\text{barnacles, piscivorous flatfishes}}^{(1)}$ $+\alpha_{\text{soft infauna, piscivorous flatfishes}}^{(1)}$
Saddleback gunnel (*Pholis ornate*) Pinpoint gunnel (*Apodichthys flavidus*) Crescent gunnel (*Pholis laeta*) Bay pipefish (*Syngnathus leptorhynchus*) Snake prickelback (*Lumpenus sagittal*) Tubesnout (*Aulorhynchus flavidus*)	Demersal fishes (+)	$-\upsilon_{\text{demersal fishes, sea lions}}^{(1)}$ $-\upsilon_{\text{demersal fishes, gulls}}^{(1)}$ $-\upsilon_{\text{demersal fishes, resident birds}}^{(1)}$ $-\upsilon_{\text{demersal fishes, migratory birds}}^{(1)}$ $-\upsilon_{\text{demersal fishes, great blue herons}}^{(1)}$ $-\upsilon_{\text{demersal fishes, migratory eagles}}^{(1)}$ $-\upsilon_{\text{demersal fishes, resident eagles}}^{(1)}$ $-\upsilon_{\text{demersal fishes, juvenile wild salmon}}^{(1)}$ $-\upsilon_{\text{demersal fishes, juvenile hatchery salmon}}^{(1)}$ $-\upsilon_{\text{demersal fishes, piscivorous flatfish}}^{(1)}$
Shiner surf perch (*Cymatogaster aggregate*)	Surfperch (+)	$-\upsilon_{\text{surfperch, resident birds}}^{(1)}$ $-\upsilon_{\text{surfperch, migratory birds}}^{(1)}$ $-\upsilon_{\text{surfperch, great blue herons}}^{(1)}$ $-\upsilon_{\text{surfperch, migratory eagles}}^{(1)}$ $-\upsilon_{\text{surfperch, resident eagles}}^{(1)}$ $-\upsilon_{\text{surfperch, juvenile wild salmon}}^{(1)}$ $-\upsilon_{\text{surfperch, juvenile hatchery salmon}}^{(1)}$ $-\upsilon_{\text{surfperch, piscivorous flatfish}}^{(1)}$ $-\upsilon_{\text{surfperch, small mouth flatfishes}}^{(1)}$ $-\upsilon_{\text{surfperch, demersal fishes}}^{(1)}$ $+\upsilon_{\text{surfperch, demersal fishes}}^{(1)}$ $-\upsilon_{\text{surfperch, YOY crab}}^{(1)}$
Red rock crab (*Cancer productus*)	Red rock crab (+)	$-\upsilon_{\text{red rock crab, gulls}}^{(1)}$ $-\upsilon_{\text{red rock crab, resident birds}}^{(1)}$ $-\upsilon_{\text{red rock crab, demersal fishes}}^{(1)}$ $+\upsilon_{\text{red rock crab, demersal fishes}}^{(1)}$ $-\upsilon_{\text{red rock crab, octopus}}^{(1)}$ $-\upsilon_{\text{red rock crab, sea stars}}^{(1)}$ $+\upsilon_{\text{red rock crab, sea stars}}^{(1)}$

continued next page

Table 1. · continued from previous page

Pacific moon snail (*Euspira lewisii*)	Predatory gastropods (-)	$-\alpha_{\text{urchins, predatory gastropods}}^{(1)}$ $-\alpha_{\text{other grazers, predatory gastropods}}^{(1)}$ $-\alpha_{\text{mussels, predatory gastropods}}^{(1)}$ $-\alpha_{\text{barnacles, predatory gastropods}}^{(1)}$ $\alpha_{\text{large infaunal bivalves, predatory gastropods}}^{(1)}$ $-\upsilon_{\text{small infaunal bivalves, predatory gastropods}}^{(3)}$ $+\upsilon_{\text{small infaunal bivalves, predatory gastropods}}^{(3)}$ $-\alpha_{\text{suspension feeders, predatory gastropods}}^{(1)}$ $-\alpha_{\text{tunicates, predatory gastropods}}^{(1)}$
Heart cockle (*Clinocardium nuttallii*)	Large infaunal bivalves (+ (1) /- (3))	$-\upsilon_{\text{large infaunal bivalves, gulls}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, gulls}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, nearshore birds}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, nearshore birds}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, migratory shorebirds}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, migratory shorebirds}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, surf perch}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, surf perch}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, piscivorous flatfishes}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, piscivorous flatfishes}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, small mouth flatfishes}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, small mouth flatfishes}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, demersal fishes}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, demersal fishes}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, octopus}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, octopus}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, YOY crab}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, YOY crab}}^{(3)}$
Heart cockle (*Clinocardium nuttallii*)	Large infaunal bivalves (+ (1) /- (3))	$-\upsilon_{\text{large infaunal bivalves, red rock crab}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, red rock crab}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, sea stars}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, sea stars}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, small crabs}}^{(1)}$ $-\upsilon_{\text{large infaunal bivalves, small crabs}}^{(3)}$ $+\upsilon_{\text{large infaunal bivalves, small crabs}}^{(3)}$ $-\upsilon_{\text{large infaunal bivalves, predatory gastropods}}^{(1)}$ $+\upsilon_{\text{large infaunal bivalves, predatory gastropods}}^{(3)}$
Corophium amphipods	Small crustaceans (- (1) /+ (3))	$-\alpha_{\text{bacteria, small crustaceans}}^{(1)}$ $+\upsilon_{\text{bacteria, small crustaceans}}^{(3)}$ $+\alpha_{\text{phytoplankton, small crustaceans}}^{(1)}$ $+\upsilon_{\text{phytoplankton, small crustaceans}}^{(3)}$ $+\alpha_{\text{benthic microalgae, small crustaceans}}^{(1)}$ $+\upsilon_{\text{benthic microalgae, small crustaceans}}^{(3)}$ $+\alpha_{\text{benthic macroalgae, small crustaceans}}^{(1)}$ $+\upsilon_{\text{benthic macroalgae, small crustaceans}}^{(3)}$ $+\alpha_{\text{eelgrass, small crustaceans}}^{(1)}$ $+\upsilon_{\text{eelgrass, small crustaceans}}^{(3)}$ $+\alpha_{\text{algal/plant matter, small crustaceans}}^{(1)}$ $+\upsilon_{\text{algal/plant matter, small crustaceans}}^{(3)}$ $+\alpha_{\text{detritus, small crustaceans}}^{(1)}$ $+\upsilon_{\text{detritus, small crustaceans}}^{(3)}$

predation (vij) decreased as a function of increasing geoduck culture (Table 1). If a prey and its predator species both had higher biomass densities inside geoduck anti-predator structure, two separate positive and negative mediation functions on the predation vulnerability of the prey species were added, as investigators could not determine how the predator–prey dynamics would play out (e.g., demersal fish prey upon surf perch and both groups had higher biomasses inside geoduck farms; Table 1). For groups that showed lower biomass densities inside geoduck plots and that were thought to be excluded (e.g., flatfishes and predatory gastropods, Table 1), their search rates (aij) were set to decrease as a function of increasing cultured geoduck biomass (Table 1). That is, they became less efficient at finding prey. These geoduck mediation effects were only applied to predator–prey functional groups found in intertidal habitats where geoduck farms are likely to be sited.

McDonald et al. (2015) found anti-predatory structure on geoduck plots to have an exclusionary effect on flatfishes and predatory gastropods (moon snail), and an attraction effect on demersal fishes (e.g., gunnels, shiner perch), small crabs, sea stars, and red rock crabs (Table 1). The small crustaceans and large infaunal bivalve groups were unique in that they had relationships to multiple geoduck stanzas (i.e., the youngest geoduck stanza associated with anti-predator structure and the oldest stanza subject to harvest). Small crustacean biomass density (based on *Corophium* amphipods) decreased in geoduck plots with anti-predator structure and was assumed to be excluded from the plots (their search rate aij decreased; Table 1). During the geoduck harvest stage, small crustacean biomass densities increased and predator refuge was assumed (their vulnerability vij decreased; Table 1). Large infaunal bivalve biomass (based on the heart cockle) increased in geoduck anti-predator structure (i.e., predator refuge; their vulnerability vij decreased) and decreased during the final, harvest stage of cultured geoducks (i.e., habitat exclusion; their search rate a_{ij} decreased; Table 1).

In the absence of empirical data on the shape and strength of these functions, the shape of all mediation functions was set to a hyperbolic function, as this is the most conservative approach (Harvey et al. 2014); the function was defined as follows:

$$\frac{M_{min}+(M_{max}+M_{min})}{1+k\cdot B} \qquad \text{Equation (4)}$$

where the endpoints are defined by M_{max} (Ecosim: Y_{zero}) and M_{min} (Ecosim: Y_{end}) and the curve has a gradient of k (Ecosim: Y_{base}). The values for each parameter were set to 2, 0, and 1, respectively, for all functional groups with the exception of small crustaceans. The small crustaceans group comprises mysid shrimps, cumaceans, benthic amphipods, and benthic isopods. Because benthic amphipods are directly targeted by a cultured geoduck mediation effect (Table 1), but make up only one third of the small crustaceans group as defined by Harvey et al. (2012a), investigators made the functional curve for this mediation effect more conservative while keeping the same hyperbolic trend by setting k to 1.5.

Analysis

The analysis consisted of two phases. The first phase entailed estimating the ecological carrying capacity for cultured geoducks in Central Puget Sound and assessing the presence of ecological thresholds related to increasing geoduck aquaculture. The second phase involved identifying trophic and non-trophic effects of geoduck culture on individual functional groups. Ecological carrying capacity is the biomass of cultured geoducks that can be supported by the existing levels of phytoplankton production (as defined by Harvey et al. 2012a) before the food web becomes unbalanced. The food web was deemed "unbalanced" when the ecotrophic efficiency of phytoplankton exceeded a value of 1 (as calculated by the mass-balance algorithm described in Equation 1); this phenomenon occurs when phytoplankton grazing mortality exceeds total productivity (Byron et al. 2011b, Jiang and Gibbs 2005).

Ecological carrying capacity was calculated by incrementally increasing the cultured geoduck biomass and associated landings until reaching the ecological carrying capacity threshold. Cultured geoduck biomass and landings were increased proportional to the base model values.

Changes in ecosystem attributes were calculated by using four established indices: the Ecosystem Reorganization Index, the Shannon Diversity Index, Mean Trophic Level (MTL), and Mixed Trophic Impact (MTI; Libralato et al. 2006, Samhouri et al. 2010). The attributes describe the capacity of an ecosystem to absorb perturbations while retaining essential structure and function, and they quantify the ecosystem impact of individual functional groups. The ecosystem reorganization index approximates ecosystem resilience (Folke et al. 2004) by measuring the extent to which perturbations cause changes in the relative biomass of individual functional groups ($B_{t,i}$) (Samhouri et al. 2009):

$$R = -\left[\sum_i \left|\frac{B_{t_2,i}-B_{t_1,i}}{\sum_i B_{t_1,i}}\right| - \left|\frac{\sum_i B_{t_2,i}-\sum_i B_{t_1,i}}{\sum_i B_{t_1,i}}\right|\right]\cdot 100 \qquad \text{Equation (5)}$$

A value of R farther from zero indicates lower resilience, implying the aggregate biomass and the individual functional groups respond differently in magnitude and direction to a pressure. This is a relative index, with zero as the lower bound (unstressed) and an unlimited upper bound (stressed) dependent on changes in biomass. Shannon Diversity Index and a biomass-weighted MTL of the food web was used as additional indicators of how changes in cultured geoduck biomass might affect overall food web structure. Lower species diversity generally indicates a more stressed ecosystem as species dominance increases and functional redundancy decreases (Odum 1985). Lower MTL indicates shorter food chains and a more stressed food web due to reduced energy flow at higher trophic levels or greater sensitivity of predators to stress or both (Odum 1985). The MTI (m_{ij}) quantifies the direct and indirect impacts of (impacting) group i on (impacted) group j across all trophic pathways that link the two groups, as calculated in Ecopath with Ecosim software. The index does not include connections via mediation functions and thus does not represent non-trophic interactions. The cumulative MTI (ε_i) was calculated to determine the net influence of each functional group on the food web following Libralato et al. (2006):

$$\varepsilon_i = \sqrt{\textstyle\sum_{j\neq i}^{n} m_{ij}^2} \qquad \text{Equation (6)}$$

The trophic and non-trophic effects of adding cultured geoduck to Central Puget Sound were evaluated by creating three versions of the model: (1) current (low) level of cultured geoducks (base model), (2) 120% cultured geoduck biomass but no geoduck mediation functions (i.e., trophic effects only), and (3) 120% cultured geoduck biomass with geoduck mediation functions (i.e., trophic and non-trophic effects). To perturb the food web, cultured geoduck biomass and associated landings were increased by 120% in 50 years. A 120% increase represented a realistic level of increase in geoduck aquaculture and was a large enough perturbation to allow examination of changes across multiple trophic levels, habitats, and life histories (e.g., birds, pelagic and demersal fishes, and invertebrates). Functional group biomass predictions from the base model (low cultured geoduck biomass) were compared with those from the model with 120% cultured geoduck biomass and no geoduck mediation effects (trophic effects only), as well as the model with 120% cultured geoduck biomass with geoduck mediation functions (trophic and non-trophic effects) to determine the possible ecological impacts of expanding geoduck aquaculture. Investigators calculated the percent change in relative biomass of each functional group in year 50. They then ran the 50-year simulations with individual mediation functions turned off to determine their specific effects on the target functional group as well as their impact on other trophically linked functional groups in the food web. Finally, they ran simulations with only individual mediation functions turned on for demersal fishes and small crustaceans to determine their influence throughout the food web. These functional groups represent important prey for a large portion of the food web and are likely to have disproportionate effects on food web dynamics.

RESULTS

A 120% increase in cultured geoduck biomass had a limited impact on phytoplankton biomass and measures of ecological resilience. The current cultured geoduck standing stock is approximately 0.1% of the estimated ecological carrying capacity in Central Puget Sound (5,928 t km^{-2}). At this threshold, the ecotrophic efficiency of phytoplankton exceeded a value of one owing to grazing mortality exceeding total phytoplankton productivity. As cultured geoduck biomass approached 120% over its initial level, the Ecosystem Reorganization Index diverged from zero by a small amount, indicating a slight reduction in stability; the Mean Trophic Level slightly increased, indicating increased stability; and the Shannon Diversity index remained constant (Table 2). The MTI was very low for cultured geoduck (ranking in the bottom 10 of all 79 functional groups) (Appendix Table 4, p. 31).

The addition of cultured geoducks into the Central Puget Sound food web without any mediation functions had very little impact on the simulated biomasses of other food web members (Appendix Table 5, p. 32). That is, after increasing the geoduck biomass by 120% over 50 years, the direct trophic effect of geoduck as a grazer on phytoplankton and as prey resource to other species was nearly negligible. The biomass densities of two geoduck predator groups, sea stars and age 4+ Dungeness crab, increased by 2% while all other food web members varied by less than 1% (Appendix Table 5). The low MTI values for cultured geoduck further support these results (Appendix Table 4).

In contrast, the addition of cultured geoduck mediation functions had a notable impact on the food web (Figure 2, Appendix Table 5). The biomass of food web members that were linked to geoduck culture through mediation functions changed considerably, with the biomass densities of some members increasing and decreasing by more than 20% (e.g., surf perches, small crabs, predatory gastropods, and small mouth flatfishes; Figure 2). In addition, changes in the biomass of food web members

Table 2. Ecosystem attributes measured in response to increased geoduck biomass in the Central Puget Sound food web. Attributes reflect system conditions at the end of 50-year simulations.

	Percent increase in geoduck biomass (tons per square kilometer)							**Unstressed state**
Attribute	20%	70%	80%	90%	100%	110%	120%	
Ecosystem Reorganization Index	0.65	2.34	2.68	3.01	3.34	3.65	3.97	Close to 0
Shannon Diversity Index	3.23	3.23	3.23	3.23	3.23	3.23	3.23	High
Change in Mean Trophic Level relative to base	0.02	0.05	0.05	0.06	0.06	0.06	0.06	High MTL

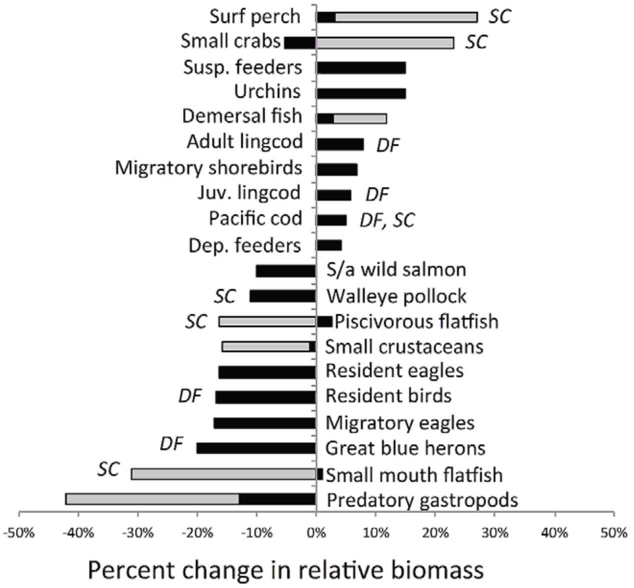


Figure 2. Functional groups with the greatest change in relative biomass between initial conditions and a simulated 120% increase in geoduck biomass over 50 years. Change in biomass resulting from targeted mediation effects (gray) or trophic connections to groups targeted by mediation effects (black) are indicated. For all but 'small crabs', effects are additive. DF (demersal fish) and SC (small crustaceans) denote if those groups are one of their top three prey (as defined by Ecosim). Relative changes in biomass for all food web members is in Appendix Table 5.

directly linked to geoduck culture propagated through the food web, contributing to additional changes in other members' biomass (Figure 2 and Appendix Table 5).

In total, the biomasses of 9 of the 10 functional groups with cultured geoduck mediation functions changed substantially and were among the top 20 groups demonstrating the greatest change in biomass (Figure 2). Red rock crab was the one exception, which showed <1% change in biomass and had a negative trend despite a positive mediation function (Appendix Table 5). Small crab biomass increased as a direct effect of the targeted mediation function and decreased without it (Figure 2). Geoduck mediation functions linked to demersal fishes and small crustaceans had substantial effects on the food web (Figure 3), supported by the high cumulative MTI values for demersal fishes and small crustaceans (ranked 11th and 25th of 79 functional groups; Appendix Table 4). For example, the cultured geoduck–demersal fish mediation function resulted in decreases in herons (-23%) and resident birds (-17%), and increases in Pacific cod (+7%) and harbor seals (+7%; Figure 3). The cultured geoduck–small crustacean mediation functions resulted in reductions in the biomasses of juvenile wild salmon (-7%) and juvenile hatchery salmon (-4%).

DISCUSSION

Food web models focused on evaluating the ecological effects of aquaculture have largely neglected non-trophic effects. This study's analysis demonstrates the importance of including non-trophic interactions when evaluating the ecological effects of shellfish aquaculture. Accounting for trophic and non-trophic interactions demonstrated that the central Puget Sound food web can support an increase in geoduck aquaculture with limited changes in individual species' biomass and ecosystem resilience at a basin scale. Also, several food web members were identified that may be substantially affected by increased geoduck culture. In contrast, models with only trophic effects of cultured geoduck predicted negligible changes in biomass for food web members due to geoduck aquaculture.

Habitat modification and facilitation are the predominant ecological effects of geoduck aquaculture in a highly productive system such as Central Puget Sound. The trophic impacts of cultured geoducks as both grazers and prey were not influential at the system level. Cultured geoducks did not substantially reduce the availability of phytoplankton for other species, as demonstrated by the small impact on ecological carrying capacity. In addition, geoduck predators (moon snails, starfish, flatfishes, red rock crab, and sea birds) are all generalists to varying degrees and showed limited change in biomass in response to increased geoduck aquaculture. However, the impact of anti-predator structure (PVC tubes and nets) placed on geoduck plots had a larger influence on the surrounding food web by providing predation refuge or by changing foraging opportunities. In turn, these effects propagated throughout the food web. The ecological effects of aquaculture structure and habitat modification have been observed for other bivalve species in a range of systems (reviewed in Coen et al. 2011). Pacific oyster on-bottom culture may reduce eelgrass densities, blade size, and growth rates (Dumbauld et al. 2009, Tallis et al. 2009), and mudflat graveling for clam cultivation may alter benthic community composition (Simenstad and Fresh 1995, Thom et al. 1994). This study suggests that efforts to understand the ecological effects of shellfish aquaculture in productive systems should go beyond modeling the direct trophic effects of bivalves and incorporate non-trophic information when possible. In addition, empirical research is required to determine the functional form and strength of these non-trophic interactions to better determine their influence on the surrounding community (Harvey 2014).

Food web members sensitive to changes in increased geoduck aquaculture represent various habitats, trophic levels, and life histories, and are candidate indicators for environmental impacts of increased bivalve aquaculture (e.g., Samhouri et al. 2009). Notably, these species were only sensitive to changes in cultured geoduck with the inclusion of non-trophic mediation effects. Some of these food web members (birds, salmon, benthic fishes) are already represented in existing and suggested indicator lists of ecosystem health for Puget Sound (Harvey et al. 2014, Kershner et al. 2011, Puget Sound Partnership 2013), which is partly due to the existence of ongoing monitoring pro-

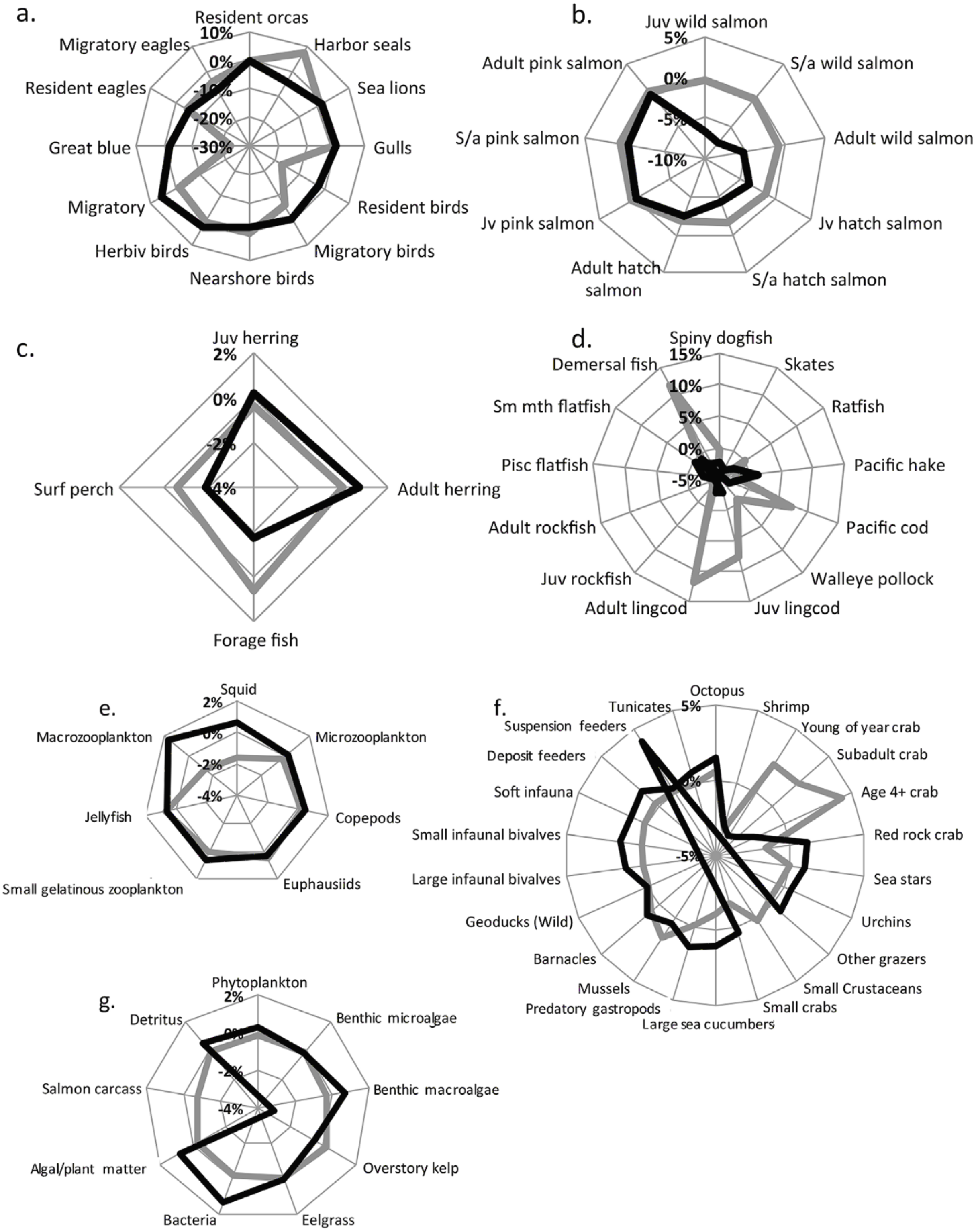


Figure 3. Percent change in relative biomass due to the addition of individual geoduck mediation effects (see Table 2 for details) on demersal fish (gray lines) and small crustaceans (black). Food web groups are divided according to: (a) marine mammals and birds, (b) salmon, (c) pelagic vertebrates, (d) benthic vertebrates, (e) pelagic invertebrates, (f) benthic invertebrates, and (g) primary producers, microbial, and detrital groups.

grams. Other species sensitive to geoduck culture (nearshore demersal fishes, small crustaceans, and flatfishes) are less consistently sampled in the region but may also prove informative as indicators. Our indicators of ecosystem structure and function (MTL, Shannon Biodiversity Index, Ecosystem Reorganization Index, and MTI) did not show conclusive trends, implying the effects of geoduck culture may be more influential at the species versus the system level. Additional diet, life history, and aquaculture interaction data for nearshore demersal fishes, small crustaceans, and various bird groups would improve the model and further refine the list of candidate ecosystem indicators for geoduck aquaculture.

The demersal fish and small crustacean functional groups were sensitive to increased cultured geoduck biomass and subsequently influenced biomass changes throughout the food web. The species' substantial bottom-up influence is due to the aggregation of multiple key prey species into single functional groups and their multiple trophic connections across the food web. The demersal fish community (e.g., poachers, eelpouts, and sculpins) is one of the most diverse and abundant in Puget Sound; however, relatively little is known of their biomass, diet, and life history (Harvey et al. 2012a, Reum and Essington 2008). In the model, demersal fishes benefit from predator refuge provided by the anti-predation structure on geoduck farms, allowing their population to increase while other predator populations (e.g., seabirds) decrease owing to lack of prey availability. Small crustaceans are one of the most important functional groups in the system, supporting the majority of bird groups, fish groups, and certain invertebrates (e.g., shrimps, octopuses, age 0+ Dungeness crabs, sea stars) (Harvey et al. 2012a). This group is one of seven functional groups that constitute 68% of the total biomass in the food web (Harvey et al. 2012a). The small crustaceans experienced a net decrease in biomass as cultured geoduck biomass increased, which was due to a negative interaction with anti-predation structure associated with cultured geoducks (although they responded positively to the harvest stage) and potentially due to an increase in predation (e.g., by surf perches and small crabs). Obtaining additional biomass, diet, and life history data and creating species-specific functional groups for demersal fishes and small crustaceans would clarify the trophic linkages responding directly to changes in cultured geoduck biomass.

The substantial decrease of most bird groups in the model is important to note, as these are important ecologically, culturally, and socio-economically. A decrease in eagle populations as cultured geoducks increase should benefit other bird groups through release from predation (Harvey et al. 2012b). However, the biomass of other birds decrease, implying bottom-up control in that they have reduced access to key prey (e.g., demersal fishes and small crustaceans) because of the predator refuge provided by anti-predator nets on geoduck farms. Migratory shore birds (biomass increase) do not primarily prey upon demersal fishes and small crustaceans and are likely benefiting from a release of eagle predation while not suffering prey depletion. Limited empirical studies have shown both negative and positive interactions between bivalve aquaculture and marine birds in other systems (Coen et al. 2011, Connolly and Colwell 2005, Kelly et al. 1996, Zydelis et al. 2009), suggesting that some interactions are likely. Further empirical study is required to understand the relationship between shellfish aquaculture and birds and validate these results.

Mediation functions in Ecosim are an important tool for incorporating non-trophic interactions into food web models and can help improve the incorporation of these data in supporting ecosystem-based approaches to aquaculture production. Although mediation functions can help incorporate habitat-specific patterns in the model, they are not equivalent to spatially-explicit models (e.g., Atlantis or Ecospace; Fulton et al. 2004a, Fulton et al. 2004b, Walters et al. 2010) and are unable to address such issues as the spatial scale of influence of geoduck farms and local community effects. For instance, shifts in the biomass of the subtidal walleye pollock and Pacific cod in response to increased cultured geoduck are most likely due to the model assumptions that demersal fishes and small crustaceans are basin-wide, continuous populations. Spatial resolution can enhance model performance (Fulton et al. 2003, Fulton et al. 2004c, Gruss et al. 2014) but may also increase uncertainty in model predictions owing to limited habitat data. Incorporating mediation functions into spatial versions of EwE (i.e., Ecospace) offers a promising area of future research as it could enable evaluation of spatially-explicit aquaculture development scenarios.

ACKNOWLEDGMENTS

Financial support was provided to Bridget E. Ferriss through a Washington State contract to Washington Sea Grant. Thanks to Joth Davis, Jim Gibbons, Tom Good, Kristin Marshall, Brian Phipps, Jameal Samhouri, and Phil Levin for helping inform the model and analysis, and improving the manuscript. We thank participants in an August 2014 workshop on shellfish aquaculture in Washington State, which was facilitated by Washington Sea Grant and supported by funds made available by Washington State.

LITERATURE CITED

Ainsworth CH, Varkey DA, Pitcher TJ (2008) Ecosystem simulations supporting ecosystem-based fisheries management in the Coral Triangle, Indonesia. Ecological Modeling 214(2-4):361-374.

Asmus RM, Asmus H (1991) Mussel beds—limiting or promoting phytoplankton. Journal of Experimental Marine Biology and Ecology148(2):215-232.

Banas NS, Hickey BM, Newton JA, Ruesink JL (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecology Progress Series 341:123-139.

Bradbury A, Tagart JV (2000) Modeling geoduck, *Panopea abrupta* (Conrad, 1849) population dynamics. II. Natural mortality and equilibrium yield. Journal of Shellfish Research 19(1):63-70.

Byron C, Link J, Costa-Pierce B, Bengtson D (2011a) Modeling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. Aquaculture 314(1-4):87-99.

Byron C, Link J, Costa-Pierce B, Bengtson D (2011b) Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modeling: Narragansett Bay, Rhode Island. Ecological Modeling 222(10):1743-1755.

Calderon-Aguilera LE, Aragon-Noriega EA, Hand CM, Moreno-Rivera VM (2010) Morphometric relationships, age, growth, and mortality of the geoduck clam, *Panopea generosa*, along the Pacific coast of Baja California, Mexico. Journal of Shellfish Research 29(2):319-326.

Cheney DP, Dewey WF, Andrew DS, Ferreira JG, Cordell JR, Davis JP (2012) Production and environmental effects of manila clam farming in north Puget Sound: Comparison of yields and responses of macro-fauna to mechanical and hand harvest. Journal of Shellfish Research 31(1):269-269.

Christensen V, Pauly D (1992) Ecopath II — A software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modeling 61(3-4):169-185.

Christensen V, Walters C (2004) Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modeling 172(2-4):109-139.

Christensen V, Walters C, Pauly D (2000) Ecopath with Ecosim: a user's guide. October 2000 edition. Fisheries Centre, University of British Columbia, Vancouver, Canada and ICLARM, Penang, Malaysia, 130 p.

Coen LD, Dumbauld B, Judge M (2011) Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish-dominated ecosystems. In Shumway SE (ed), Shellfish Aquaculture and the Environment. Wiley-Blackwell, pp. 239-295.

Connolly LM, Colwell MA (2005) Comparative use of longline oysterbeds and adjacent tidal flats by waterbirds. Bird Conservation International 15(3):237-255.

Cranford PJ, Kamermans P, Krause G, et al. (2012) An ecosystem-based approach and management framework for the integrated evaluation of bivalve aquaculture impacts. Aquactic Environmental Interactions 2(3):193-213.

Dubois S, Marin-Leal JC, Ropert M, Lefebvre S (2007) Effects of oyster farming on macrofaunal assemblages associated with *Lanice conchilega* tubeworm populations: a trophic analysis using natural stable isotopes. Aquaculture 271(1-4):336-349.

Dumbauld BR, Ruesink JL, Rumrill SS (2009) 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. Aquaculture 290(3-4):196-223.

Espinosa-Romero MJ, Gregr EJ, Walters C, Christensen V, Chan KMA (2011) Representing mediating effects and species reintroductions in Ecopath with Ecosim. Ecological Modeling 222(9):1569-1579.

Faulkner H (2013) Influence of mariculture on winter sea duck distribution and abundance in South Puget Sound. MS thesis, Evergreen College, Olympia, WA.

Folke C, Carpenter S, Walker B, et al. (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annual Review of Ecology, Evolution, and Systematics 35:557-581.

Fulton EA, Parslow JS, Smith ADM, Johnson CR (2004a) Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. Ecological Modeling 173(4):371-406.

Fulton EA, Smith ADM, Johnson CR (2004b) Biogeochemical marine ecosystem models I: IGBEM — a model of marine bay ecosystems. Ecological Modeling 174(3):267-307.

Fulton EA, Smith ADM, Johnson CR (2004c) Effects of spatial resolution on the performance and interpretation of marine ecosystem models. Ecological Modeling 176(1-2):27-42.

Fulton EA, Smith ADM, Johnson CR (2003) Effect of complexity on marine ecosystem models. Marine Ecology Progress Series 253:1-16.

Gruss A, Drexler M, Ainsworth CH (2014) Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research 159:11-24.

Harvey CJ (2014) Mediation functions in Ecopath with Ecosim: handle with care. Canadian Journal of Fisheries and Aquatic Sciences 71(7):1020-1029.

Harvey C, Garfield N, Hazen E, Williams GD (2014) The California Current Integrated Ecosystem Assessment: Phase III Report. Available at http://www.noaa.gov/iea/CCIEA-Report/pdf/.

Harvey CJ, Williams GD, Levin PS (2012a) Food web structure and trophic control in central Puget Sound. Estuaries and Coasts 35(3):821-838.

Harvey CJ, Good TP, Pearson SF (2012b) Top-down influence of resident and overwintering Bald Eagles (*Haliaeetus leucocephalus*) in a model marine ecosystem. Canadian Journal of Zoology 90(7):903-914.

Jiang WM, Gibbs MT (2005) Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. Aquaculture 244(1-4):171-185.

Kelly J, Evens J, Stallcup R, Wimpfheimer D (1996) Effects of aquaculture on habitat use by wintering shorebirds in Tomales Bay, California. California Fish and Game 82(4):160-174.

Kershner J, Samhouri JF, James CA, Levin PS (2011) Selecting indicator portfolios for marine species and food webs: a Puget Sound case study. PLoS One 6(10):12.

Leloup FA, Desroy N, Le Mao P, Pauly D, Le Pape O (2008) Interactions between a natural food web, shellfish farming and exotic species: The case of the Bay of Mont Saint Michel (France). Estuarine, Coastal and Shelf Science 76(1):111-120.

Libralato S, Christensen V, Pauly D (2006) A method for identifying keystone species in food web models. Ecological Modelling 195:153-171.

Ma HG, Townsend H, Zhang XS, Sigrist M, Christensen V (2010) Using a fisheries ecosystem model with a water quality model to explore trophic and habitat impacts on a fisheries stock: A case study of the blue crab population in the Chesapeake Bay. Ecological Modeling 221(7):997-1004.

McDonald P, Galloway A, McPeek K, VanBlaricom G (2015) Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington, USA. Journal of Shellfish Research 34(1):189-202. McDonald PS, Stevick PF, Galloway AWE,

McPeek K, Armstrong DA, VanBlaricom GR (2012) Nekton, nets, and tubes: Macrofauna response to intertidal geoduck aquaculture operations in Puget Sound, Washington, USA. Journal of Shellfish Research 31(1):320-320.

NRC (National Research Council) (2010) Ecosystem Concepts for Sustainable Bivalve Mariculture. Washington, DC, 190 p.

Odum, EP (1985) Trends expected in stressed ecosystems. Bioscience 35(7):419-422.

Plummer ML, Harvey CJ, Anderson LE, Guerry AD, Ruckelshaus MH (2013) The role of eelgrass in marine community interactions and ecosystem services: results from ecosystem-scale food web models. Ecosystems 16(2):237-251.

Polovina, JJ (1984) Model of a coral-reef ecosystem. 1. The Ecopath model and its application to French Frigate Shoals. Coral Reefs 3(1):1-11.

Price J, VanBlaricom G, McDonald PS (2012) Effects of harvest activity on infaunal communities in geoduck clam aquaculture plots in southern Puget Sound, Washington, USA. Journal of Shellfish Research 31(1):334-334.

Puget Sound Partnership (2013) 2013 State of the Sound: A Biennial Report on the Recovery of Puget Sound. Tacoma, Washington, 177 p.

Reum JCP, Essington TE (2008) Seasonal variation in guild structure of the Puget Sound demersal fish community. Estuaries and Coasts 31:790-801.

Samhouri JF, Levin PS, Ainsworth CH (2010) Identifying thresholds for ecosystem-based management. PLoS One 5(1):10.

Samhouri JF, Levin PS, Harvey CJ (2009) Quantitative evaluation of marine ecosystem indicator performance using food web models. Ecosystems 12(8):1283-1298.

Simenstad CA, Fresh KL (1995) Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries — scales of disturbance. Estuaries 18(1A):43-70.

Tallis HM, Ruesink JL, Dumbauld B, Hacker S, Wisehart LM (2009) Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research 28(2):251-261.

Thom RM, Parkwell TL, Niyogi DK, Shreffler DK (1994) Effects of graveling on the primary productivity, respiration and nutrient flux of two estuarine tidal flats. Marine Biology 118(2):329-341.

Vanblaricom GR, Eccles JL, Olden JD, McDonald PS (2015) Ecological effects of the harvest phase of geoduck (*Panopea generosa* Gould, 1850) aquaculture on infaunal communities in Southern Puget Sound, Washington. Journal of Shellfish Research 34(1):171-187.

Walters C, Christensen V, Walters W, Rose K (2010) Representation of multistanza life histories in Ecospace models for spatial organization of ecosystem trophic interaction patterns. Bulletin of Marine Science 86(2):439-459.

Wootton, JT (1994) The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443-466.

Zhou Y, Yang HS, Zhang T et al. (2006) Influence of filtering and biodeposition by the cultured scallop *Chlamys farreri* on benthic-pelagic coupling in a eutrophic bay in China. Marine Ecology Progress Series 317:127-141.

Zydelis, R, Esler, D, Kirk, M, Boyd, WS (2009) Effects of off-bottom shellfish aquaculture on winter habitat use by molluscivorous sea ducks. Aquatic Conservation: Marine and Freshwater Ecosystems 19(1):34-42.

APPENDIX

Additional Details on Methods and Results

Appendix Table 1. Functional groups in the Ecopath with Ecosim (EwE) model with major representatives.

Functional group	**Common name**	**Scientific classification**
Harbor seals	Harbor seal	*Phoca vitulina*
Sea lions	California sea lion	*Zalophus californianus*
	Steller sea lion	*Eumetopias jubatus*
Gulls	Various gulls	*Larus* spp.
Resident diving birds	Various cormorants	*Phalacrocorax* spp.
	Pigeon guillemot	*Cepphus columba*
Migratory diving birds	Western grebe	*Aechmophorus occidentalis*
	Various loons	*Gavia* spp.
	Common murre	*Uria aalga*
Nearshore diving birds	Various scoters	*Melanitta* spp.
	Various goldeneyes	*Bucephala* spp.
Herbivorous birds	Dabbling ducks	*Anas* spp.
	Various geese	*Branta* spp.
Migratory shorebirds	Dunlin	*Calidris alpina*
Great blue herons	Great blue herons	*Ardea herodias*
Raptors	Bald eagle	*Haliaeetus leucocephalus*
Wild salmon	Chum salmon	*Oncorhynchus keta*
	Chinook salmon	*O. tshawytscha*
	Coho salmon	*O. kisutch*
Hatchery salmon	Chum salmon	*O. keta*
	Chinook salmon	*O. tshawytscha*
	Coho salmon	*O. kisutch*
Pink salmon	Pink salmon	*O. gorbuscha*
Pacific herring	Pacific herring	*Clupea pallasii*
Forage fishes	Surf smelt	*Hypomesus pretiosus*
	Pacific sand lance	*Ammodytes hexapterus*
Surfperches	Shiner perch	*Cymatogaster aggregata*
	Striped seaperch	*Embiotoca lateralis*
Spiny dogfish	Spiny dogfish	*Squalus acanthias*
Skates	Longnose skate	*Raja rhina*
	Big skate	*R. binoculata*
Ratfish	Whitespotted ratfish	*Hydrolagus colliei*
Pacific hake	Pacific hake	*Merluccius productus*
Pacific cod	Pacific cod	*Gadus macrocephalus*
Walleye pollock	Walleye pollock	*Theragra chalcogramma*
Lingcod	Lingcod	*Ophiodon elongatus*
Rockfishes	Copper rockfish	*Sebastes caurinus*
	Quillback rockfish	*S. maliger*
Piscivorous flatfishes	Pacific sanddab	*Citharichthys sordidus*
Small-mouthed flatfishes	English sole	*Parophrys vetulus*
	Rock sole	*Lepidopsetta bilineata*
Demersal fishes	Various poachers	Family Agonidae
	Various eelpouts	*Lycodes* spp.
	Various small sculpins	Family Cottidae
Squid	Opalescent (market) squid	*Loligo opalescens*
Octopuses	Red octopus	*Octopus rubescens*
	Giant Pacific octopus	*Enteroctopus dofleini*
Shrimp	Pandalid shrimp	Family Pandalidae
	Sand shrimp	*Crangon* spp.
Cancer crab	Dungeness crab	*Cancer magister*
Red rock crab	Red rock crab	*Cancer productus*

Appendix Table 1 • continued

Functional group	Common name	Scientific classification
Sea stars	Sunflower star	*Pycnopodia helianthoides*
	Pink sea star	*Pisaster brevispinis*
Sea urchins	Green sea urchin	*Strongylocentrotus droebachiensis*
	Red sea urchin	*S. franciscanus*
Other grazers	Various snails	Class Gastropoda
	Various chitons	Class Polyplacophora
Small crustaceans	Various amphipods	Suborders Gammaridea, Corophiidea
	Various mysids	Family Mysidae
Small crabs	Various crabs	Infraorders Brachyura, Anomura
Large sea cucumbers	California sea cucumber	*Parastichopus californicus*
Predatory gastropods	Moon snail	*Euspira lewisii*
	Hairy triton	*Fusitriton oregonensis*
Mussels	Blue mussel	*Mytilus edulis*
Barnacles	Various barnacles	Suborder Balanomorpha
Geoduck	Geoduck	*Panopea abrupta*
Cultured geoduck	Geoduck	*Panopea generosa*
Large infaunal bivalves	Butter clam	*Saxidomus gigantea*
	Horse clam	*Tresus capax*
	Native littleneck clam	*Leukoma staminea*
	Manila clam	*Venerupis philippinarum*
Small infaunal bivalves	Purple *Transennella*	*Transennella tantilla*
	Amethyst gemclam	*Gemma gemma*
	Charlotte macoma	*Macoma carlottensis*
	Baltic macoma	*Macoma balthica*
Soft infauna	Polychaetes	Class Polychaeta
Deposit feeders	Brittle star	*Amphiodia urtica*
	Various sea cucumbers	Class Holothuroidea
Suspension feeders	Various sponges	Phylum Porifera
	Various bryozoans	Phylum Bryozoa
	Sea pen	*Ptilosarcus gurneyi*
Tunicates	Various sea squirts	Class Ascidiacea
Bacteria	Various bacteria	
Microzooplankton	Various microzooplankton	
Copepods	Various copepods	Order Calanoida
Euphausiids	Pacific krill	*Euphausia pacifica*
Small gelatinous zooplankton	Various small jellyfish, ctenophores, and other soft plankton	
Jellyfishes	Lion's mane jelly	*Cyanea capillata*
	Moon jelly	*Aurelia labiata*
	Fried egg jelly	*Phacellophora camtschatica*
Macrozooplankton	Various planktonic shrimp, amphipods, and larval crustaceans	
Phytoplankton	Various diatoms, dinoflagellates and phytoflagellates	
Benthic microalgae	Various benthic diatoms	
Benthic macroalgae	Various understory algal species	
Overstory kelp	Bull kelp	*Nereocystis luetkeanus*
Eelgrass	Native eelgrass	*Zostera marina*
Detritus	Not available	
Plant/algal material	Not available	
Salmon carcasses	Not available	*Oncorhynchus* spp.

Appendix Table 2. Parameters for new functional groups in the central Puget Sound EwE model, including trophic level (TL), biomass (B: metric tons per square kilometer), production to biomass ratio (P/B: per year), ecotrophic efficiency (EE) and production to consumption ratio (P/Q). Values in bold were calculated by the mass-balancing routine in the Ecopath model.

Group	TL	B	P/B	Q/B	EE	P/Q
Migratory shorebirds	3.660	0.039E-03[1]	0.370[2]	456.400[3]	0.222	0.005
Great blue heron	4.453	0.025E-01[4]	0.390[5]	72.310[6]	0.222	0.005
Red rock crab	3.110	1.859	1.100[7]	3.666[8]	0.900[8]	0.300
Small crustaceans	2.044	20.143	3.410[9]	25.000[8]	0.900[8]	0.136
Small crabs	2.283	15.921	0.820[10]	2.730[8]	0.800[10]	0.300
Cultured geoduck(yr1-2)	2.025	0.195[11]	0.143[12]	3.977[8]	0.434	0.036
Cultured geoduck(yr3-5)	2.025	3.542[11]	0.080[12]	1.849[8]	0.044	0.043
Cultured geoduck(yr6-7)	2.025	2.870[11]	1.000[12]	1.357[8]	0.043	0.737
Large infaunal bivalves	2.050	74.860[13]	1.010[8]	3.367[8]	0.118	0.300
Small infaunal bivalves	2.050	54.680[14]	2.059[8]	6.863[8]	0.476	0.300

[1] *Dalsgaard et al. 1998, Evenson and Buchanan 1997, Macwhirter et al. 2002*

[2] *Macwhirter et al. 2002, Warnock and Gill 1996*

[3] *Brennan 1990, Hunt 2000, Warnock and Gill 1996*

[4] *Eissinger 2007*

[5] *Butler 1997*

[6] *Butler 1995*

[7] *Parker 2002*

[8] *Harvey et al. 2012*

[9] *McLusky and McIntyre 1988*

[10] *Aydin et al. 2007*

[11] *Bradbury and Tagart 2000, Calderon-Aguilera et al. 2010, Hoffmann et al. 2000; Washington Department of Fish & Wildlife, personal communication*

[12] *J Gibbons, Taylor Shellfish, personal communication; B Phipps, Seattle Shellfish, personal communication*

[13] *Dethier 2012*

[14] *Partridge et al. 2005*

Appendix Table 3. Revised diet matrix for functional groups in the central Puget Sound model. Each column represents the diet proportions of a consumer and sums to 1. Asterisk (*) < 0.001. Please see *https://wsg.washington.edu/Ferriss-Appendix-Table-3*

Appendix Table 4. Cumulative Mixed Trophic Impact (MTI) of each functional group in order from highest to lowest impact.

Functional Group	Cumulative MTI	Rank
Phytoplankton	1.46	1
Resident eagles	1.31	2
Detritus	1.29	3
Other grazers	1.12	4
Spiny dogfish	1.05	5
Large infaunal bivalves	1.04	6
Copepods	0.94	7
Migratory eagles	0.91	8
Soft infauna	0.87	9
Ratfish	0.85	10
Demersal fishes	0.85	11
Small mouth flatfishes	0.83	12
Gulls	0.81	13
Microzooplankton	0.73	14
Harbor seals	0.71	15
Shrimp	0.68	16
Euphausiids	0.61	17
Small infaunal bivalves	0.59	18
Predatory gastropods	0.59	19
Bentich macroalgae	0.59	20
Red rock crab	0.59	21
Benthic microalgae	0.59	22
Mussels	0.57	23
Macrozooplankton	0.57	24
Small Crustaceans	0.56	25
Bacteria	0.54	26
Sea lions	0.53	27
Subadult crab	0.52	28
Adult lingcod	0.51	29
Surf perch	0.49	30
Juvenile herring	0.46	31
Subadult wild salmon	0.38	32
Walleye pollock	0.37	33
Herbivorous birds	0.37	34
Piscivorous flatfishes	0.35	35
Migratory birds	0.34	36
Salmon carcass	0.32	37
Adult hatch salmon	0.32	38
Nearshore birds	0.31	39
Subadult hatchery salmon	0.30	40
Forage fishes	0.30	41
Jellyfishes	0.27	42
Suspension feeders	0.25	43
Adult herring	0.24	44
Octopus	0.22	45
Sea stars	0.21	46
Small gelatenous zooplankton	0.20	47
Small crabs	0.20	48
Adult wild salmon	0.18	49
Squid	0.17	50
Urchins	0.17	51
Barnacles	0.16	52
Algal/plant matter	0.16	53
Pacific hake	0.15	54
Deposite feeders	0.14	55
YOY crab	0.13	56
Resident birds	0.12	57
Resident orcas	0.10	58
Eelgrass	0.10	59
Juvenile lingcod	0.09	60
Juvenile rockfishes	0.08	61
Pacific cod	0.08	62
Skates	0.08	63
Adult rockfishes	0.06	64
Overstory kelp	0.05	65
Juvenile hatchery salmon	0.03	66
Age 4+ crab	0.02	67
Great blue herons	0.02	68
Adult pink salmon	0.02	69
Juvenile wild salmon	0.02	70
Geoducks (Wild)	0.02	71
Large sea cucumbers	0.01	72
Juvenile pink salmon	0.00	73
Geoduck_yr3-5(cultured)	0.00	74
Tunicates	0.00	75
Geoduck_yr1-2(cultured)	0.00	76
Geoduck_yr6-7(cultured)	0.00	77
Migratory shorebirds	0.00	78
Subadult pink salmon	0.00	79

Appendix Table 5. Predicted relative biomass after cultured geoducks are increased by 120% over 50 years in the central Puget Sound with and without geoduck mediation functions. Biomass is relative to the base model (e.g., a value of 1 is equivalent to no change).

	Relative Biomass		
Functional Group	With Geoduck Mediation	No Geoduck Mediation	% Difference
Marine Mammals			
Resident orcas	1.000	0.993	-0.70%
Harbor seals	0.999	1.010	1.07%
Sea lions	1.000	0.950	-5.00%
Birds			
Gulls	0.999	0.990	-0.85%
Resident birds	0.998	0.829	-16.92%
Migratory birds	0.999	0.952	-4.72%
Nearshore birds	1.001	0.950	-5.06%
Herbivorous birds	1.000	1.032	3.21%
Migratory shorebirds	0.997	1.066	6.87%
Great blue herons	0.998	0.798	-19.97%
Resident eagles	1.000	0.836	-16.42%
Migratory eagles	1.006	0.836	-17.02%
Salmon			
Juvenile wild salmon	1.000	0.910	-8.94%
Subadult wild salmon	0.999	0.898	-10.17%
Adult wild salmon	1.000	0.923	-7.70%
Juvenile hatch salmon	1.000	0.938	-6.20%
Subadult hatch salmon	0.999	0.925	-7.46%
Adult hatch salmon	1.001	0.949	-5.26%
Juvenile pink salmon	1.000	0.992	-0.73%
Subadult pink salmon	0.999	0.988	-1.10%
Adult pink salmon	1.001	0.997	-0.39%
Pelagic fish			
Juvenile herring	1.000	1.003	0.29%
Adult herring	1.000	1.009	0.93%
Forage fishes	0.998	0.962	-3.61%
Surf perches	0.999	1.268	26.95%
Pacific hake	0.999	1.008	0.87%
Demersal fishes			
Spiny dogfish	0.999	0.935	-6.39%

	Relative Biomass		
Functional Group	With Geoduck Mediation	No Geoduck Mediation	% Difference
Skates	1.000	0.966	-3.40%
Ratfish	1.000	0.993	-0.63%
Pacific cod	0.999	1.049	4.96%
Walleye pollock	1.000	0.890	-10.98%
Juvenile lingcod	1.001	1.058	5.64%
Adult lingcod	1.001	1.080	7.82%
Juvenile rockfishes	1.000	0.975	-2.54%
Adult rockfishes	1.000	0.976	-2.40%
Piscivorous flatfishes	1.001	0.864	-13.69%
Small mouth flatfishes	1.000	0.701	-29.91%
Demersal fishes	0.999	1.116	11.68%
Demersal invertebrates			
Octopus	1.000	0.959	-4.11%
Shrimp	1.000	0.980	-1.95%
YOY crab	1.000	0.964	-3.62%
Subadult crab	1.000	0.970	-2.94%
Age 4+ crab	1.000	1.035	3.46%
Red rock crab	1.002	1.006	0.43%
Sea stars	1.010	0.995	-1.55%
Urchins	0.999	1.147	14.81%
Other grazers	1.000	1.017	1.65%
Small Crustaceans(new)	1.000	0.841	-15.85%
Small crabs	1.000	1.178	17.79%
Large sea cucumbers	0.999	1.009	1.04%
Predatory gastropods	1.000	0.580	-41.99%
Mussels	0.999	0.963	-3.65%
Barnacles	0.999	0.998	-0.15%
Geoducks (Wild)	1.000	1.003	0.30%
Geoduck_yr1-2(cultured)	1.919	2.201	28.22%
Geoduck_yr3-5(cultured)	3.043	2.200	-84.34%
Geoduck_yr6-7(cultured)	2.200	2.200	0.00%
Large infaunal bivalves	1.000	1.039	3.95%
Small infaunal bivalves	1.000	0.987	-1.31%
Soft infauna	1.000	1.033	3.33%
Deposit feeders	1.000	1.041	4.12%
Suspension feeders	0.999	1.148	14.92%

Appendix Table 5 · continued

	Relative Biomass		
Functional Group	With Geoduck Mediation	No Geoduck Mediation	% Difference
Pelagic invertebrates			
Squid	0.999	0.990	-0.91%
Tunicates	0.999	1.030	3.09%
Microzooplankton	1.000	1.005	0.52%
Copepods	0.999	1.000	0.10%
Euphausiids	0.999	1.004	0.50%
Small gelatinous zooplankton	1.000	1.007	0.71%
Jellyfish	0.999	1.002	0.37%
Macrozooplankton	0.999	1.001	0.19%
Primary producers			
Phytoplankton	1.000	1.004	0.41%
Benthic microalgae	1.000	0.979	-2.08%
Benthic macroalgae	1.000	0.982	-1.86%
Overstory kelp	1.000	0.958	-4.17%
Eelgrass	1.000	0.998	-0.19%
Microbial and detrital			
Bacteria	1.000	1.004	0.42%
Algal/plant matter	1.000	0.974	-2.62%
Salmon carcass	1.000	0.927	-7.29%
Detritus	1.000	1.004	0.41%

Qualitative Network Models in Support of Ecosystem Approaches to Aquaculture Production: Potential Applications to Management and Climate Change

Jonathan CP Reum, Bridget E Ferriss, Washington Sea Grant; P Sean McDonald, University of Washington (UW) School of Aquatic and Fishery Sciences; Dara Farrell, UW Department of Mechanical Engineering; Chris J Harvey, NOAA Fisheries, Northwest Fisheries Science Center, Conservation Biology Division

ABSTRACT

Predicting the effects of aquaculture development in coastal ecosystems remains challenging, and tools that account for complex ecological interactions are needed to support ecosystem approaches to aquaculture. In this study, investigators used qualitative network models (QNMs) to examine the potential community effects of increasing bivalve aquaculture in South Puget Sound and Willapa Bay, Washington. QNMs are formalized conceptual models that require only a qualitative understanding of how variables composing a system interact (that is, the sign of interactions: +, –, and 0) and are, therefore, well suited to data-limited systems. The versatility of the approach was demonstrated by examining different sets of scenarios for each system. For South Puget Sound, community-wide responses to scenarios in which bivalve cultivation effort increased for three different bivalve species (Manila clam *Venerupis philippinarum*, Pacific oyster *Crassostrea* gigas, and geoduck *Panopea generosa*) were examined. Further evaluations addressed community-wide responses to the removal of benthic bivalve predators, a future increase in nutrient loadings, and combinations of these scenarios acting simultaneously. The scenarios enabled identification of potential tradeoffs between increased aquaculture and shifts in the abundance of community members and assessment of the possible effects of different management actions. For Willapa Bay, the investigators evaluated the potential implications of different hypothesized OA effects on the main cultivated species (Pacific oyster, Manila clam) as well as the community as a whole. In addition, identified key interactions that influence the sign outcome of community responses to press perturbations were identified, highlighting potential points for management intervention and linkages deserving of more focused quantitative study. QNMs are mathematically robust and highly flexible but remain underutilized. They may serve as valuable tools for supporting ecosystem approaches to aquaculture.

INTRODUCTION

Shellfish aquaculture production has increased rapidly worldwide and supplies protein to meet growing human demands as well as jobs and income that benefit coastal economies (National Research Council 2010). In some regions of Washington State, shellfish aquaculture has taken place for more than a century, but the industry is evolving in terms of growout methods and the variety of species cultivated. As the industry expands, the conversion of coastal habitat to shellfish farms has raised interest in understanding the potential ecological effects, positive and negative, on coastal ecosystems.

At the same time, coastal ecosystems are increasingly under pressure owing to a variety of issues including shoreline development, reduced water quality, overfishing, and climate change. Because cultured shellfish are integrated within and dependent upon healthy coastal ecosystems, shifts in one or a few components of the food web may have consequences for shellfish production. To better understand the effects of aquaculture on the environment and environmental changes on aquaculture, modeling approaches are needed that account for the complex network of ecological interactions that influence system behavior.

Quantitative food web models offer one framework for modeling complex systems and can help facilitate ecosystem approaches to aquaculture production. These models can facilitate a more holistic perspective on management decisions by capturing the response of the community to different perturbation scenarios (Byron et al. 2011, Jiang and Gibbs 2005). Although significant headway has been made in developing quantitative food web models for Central Puget Sound (Ferriss et al. 2015, Harvey et al. 2012), in general, their parameterization requires large amounts of data and can be expensive and time-consuming (McKindsey et al. 2006, Plaganyi and Butterworth 2004). Consequently, their application to more data-poor regions of the state is challenging. In contrast, Qualitative Network Models (QNMs) and the closely related "loop analysis" are well suited for modeling data-poor systems (Puccia and Levins 1985). QNMs were first developed to facilitate the analysis of feedbacks in network models (Levins 1974, Puccia and Levins 1985) and require only a qualitative understanding of the relationships linking species and variables within a system: that is, information on only the sign of interactions between variables (+, -, or 0) are needed. The method permits the rapid assembly of hypotheses of system structure and provides qualitative predictions of the response of community members to a sustained change, or press perturbation (Bender et al. 1984), in any system variable(s).

In QNMs, the predicted responses are qualitative, and therefore imprecise, but this can be considered advantageous because it de-emphasizes precise measurements of model parameters, which in practice are often difficult or impossible to obtain (Dambacher et al. 2009). Instead, the model focuses effort on describing general relationships among variables, which is typically more feasible for complex ecosystems (Dambacher et al. 2009, Levins 1998). Given their versatility, QNMs have been used in a range of different ecological applications including predicting community-level effects of eutrophication (Carey et al. 2014, Lane and Levins 1977), habitat disturbance (Dambacher et al. 2007), fishing (Metcalf 2010, Ortiz and Wolff 2002), species invasions and eradications (Castillo et al. 2000, Raymond et al. 2011), and assessing the effects of climate change on ecosystems (Dambacher et al. 2010, Melbourne-Thomas et al. 2013). However, QNMs have seen only limited application in the context of aquaculture (e.g., Whitlatch and Osman 1994).

In this study, QNMs were built that correspond with South Puget Sound and Willapa Bay (Figure 1). This enabled the investigators to summarize system knowledge and use the models to explore the potential effects of changes in aquaculture or the food web on cultured species and the community as a whole. For the South Puget Sound QNM, three different types of scenarios were examined: First, potential community-wide responses to increased aquaculture were examined, with the goal being to identify potential tradeoffs between bivalve species and the abundance of other community members. Second, investigators examined whether reducing benthic bivalve predators in the system (for instance, through targeted fisheries or manual removal) might improve bivalve production. Last, given predictions that nitrogen inputs are likely to increase in South Puget Sound (Ahmed et al. 2014, Roberts et al. 2014), scenarios of increased nutrient concentrations on cultured bivalves and the community were evaluated.

The Willapa Bay study focused on evaluating the potential effects of changes in seawater carbonate chemistry resulting from ocean uptake of anthropogenic atmospheric CO_2 (ocean acidification, OA) on key members of the food web. Specifically, three potential OA impacts were simulated: increased primary production, reduced production of bivalves, and enhanced predation by crabs and gastropods on bivalves. Qualitative examinations were conducted on how OA impacts on individual species propagate through the community and which interactions were most influential in determining the overall impact of OA.

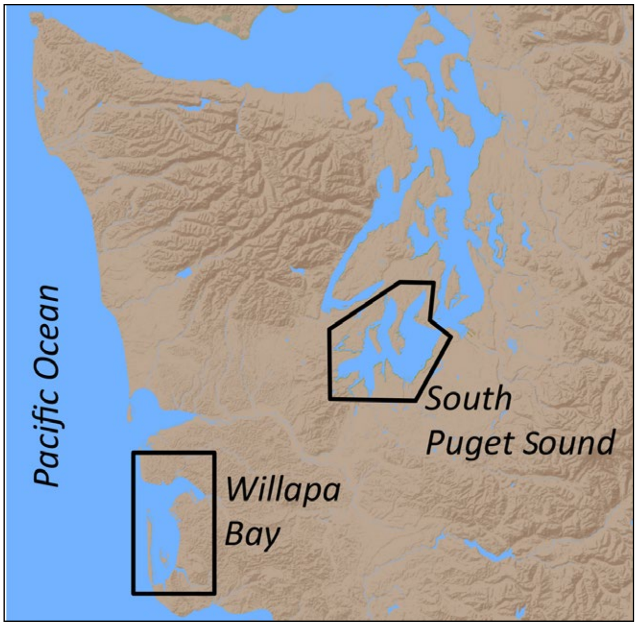


Figure 1. Location of Willapa Bay and South Puget Sound. Qualitative network models (QNMs) describing shellfish–food web interactions were developed for both regions.

MATERIALS AND METHODS

Study Site Overview

South Puget Sound

South Puget Sound is a large (449 square kilometers, 37 meters mean depth) subbasin of Puget Sound; approximately 15% of the basin is tidelands by area (Figure 1a, Burns 1985). South Puget Sound supports a diverse ecological community that includes marine mammals, migratory waterfowl, species of management and conservation concern (e.g., the eelgrass *Zostera marina*, Chinook salmon *Oncorhynchus tshawytscha*) as well as commercial, tribal, and recreational capture fisheries (e.g., Chinook salmon, Dungeness crab *Cancer magister*). Cultivation of non-native Pacific oyster *Crassostrea gigas* began in the 1920s after the collapse of native Olympia oyster *Ostrea lurida* populations. Manila clam *Venerupis philippinarum*, which may have been accidentally introduced with oysters brought from Japan, became a focus of cultivation efforts in the 1940s. Commercial culture of geoduck *Panopea generosa* was developed in the early 1990s to augment lucrative wild harvest in subtidal areas and has since increased dramatically. Recent reported shellfish aquaculture landings have approached 1,500,000 kilograms per year and consist of Pacific oyster (55%), Manila clam (23%), and geoduck (16%), with remaining landings (10%) composed of assorted non-native bivalves (blue mussel *Mytilus spp.*, European oyster *Ostrea edulis*, eastern oyster *Crassostrea virginica*, Kumamoto oyster *Crassostrea sikamea)* and native Olympia oyster (shellfish aquaculture landings statistics for 2010, Washington Department of Fish & Wildlife).

Willapa Bay

Willapa Bay is the largest estuary on the outer Washington coast (260 km^2) and has extensive tidelands (greater than 50% of the bay by area) that have supported commercial shellfish aquaculture for more than a century (Feldman et al. 2000). The estuary is an important region for cultivating the non-native Pacific oyster and supplies ~10% of all oysters consumed domestically (Ruesink et al. 2006). In addition, the introduced Manila clam is also intensively cultivated. Apart from cultivated shellfish, the estuary also supports a wild fishery for Dungeness crab and provides habitat to species of management and conservation concern including threatened fishes (Chinook salmon, green sturgeon *Acipenser medirostris*) and migratory waterfowl (black brant *Branta bernicla nigricans*). During the spring and summer months, northerly winds result in the upwelling of nutrient-rich waters along the open coast which, in turn, promote high rates of primary production and dense standing stocks of phytoplankton that circulate into the estuary, supporting secondary production (Banas et al. 2007, Hickey and Banas 2003).

Like many other estuaries, levels of partial pressure CO_2 (pCO_2) in Willapa Bay range widely, from 300 to 4,000 microatmospheres (µatm; for reference, current atmospheric pCO_2 is ~400 µatm), and vary spatially, with the highest values occurring up-estuary and in association with low-salinity waters (Ruesink et al. 2015). Carbonate chemistry dynamics in Willapa Bay are more variable than open ocean systems and are strongly influenced by freshwater inputs, rates of photosynthesis, and processes that influence the abundance and remineralization of organic material (Ruesink et al. 2015). However, marine carbonate chemistry conditions in Willapa Bay are also partly influenced by atmospheric pCO_2 levels, as are conditions in adjoining coastal waters (Feely et al. 2008). Consequently, pCO_2 levels in Willapa Bay are likely to increase over the long term (years to decades) with increasing atmospheric pCO_2, assuming that watershed processes and community metabolism also remain stable over time (Borges and Abril 2011, Duarte et al. 2013).

Qualitative Network Models: Background

QNMs are a special type of graph — known as a digraph — that consist of variables and linkages or, equivalently, nodes and edges (Puccia and Levins 1985). The linkages in the graph correspond to a matrix of interactions that, in ecology, typically represent trophic interactions. However, linkages can also represent other ecological interactions such as competition and facilitation or interactions between species or any other type of variable (e.g., abiotic, social, economic). The analysis of QNMs draws upon graph theory and matrix algebra and is based specifically on analysis of the community matrix (Levins 1974, Puccia and Levins 1985).

A central premise of the approach is that the per capita change in a species or the level of some non-species variable can be described as a continuous function of the other variables in the system. The dynamics of n interacting variables can be represented as a set of ordinary differential equations, where for each variable x (I = 1, 2, ..., n):

$$\frac{dx_i}{dt} = f_i(x_1, x_2, \ldots, x_n;\ c_1, c_2, \ldots, c_n)$$

That is, the growth rate of variable x_i is a function of the levels of some or all variables in the system, and usually itself, and a set of growth parameters *c*. In the case of species variables, their *c* parameters may correspond with birth, death, or immigration rates. The interaction coefficient a_{ij} measures the direct effect of a small change in the level of variable *j* on the growth rate of variable *i*, and is defined as the partial derivative of f_i with respect to x_i (Bender et al. 1984):

$$a_{ij} = \partial f_i / \partial x_j$$

Although the effects of x_j on x_i may not necessarily be linear, the approach assumes that the dynamics of each variable can be adequately approximated by a linearization near equilibrium levels (Stone and Roberts 1991). The *i* × *j* matrix containing the a_{ij} elements is the community interaction matrix **A**. The negative inverse of **A** can be used to estimate the long-term effects of a press perturbation, which is defined as a sustained shift in the magnitude of a species' growth parameter (Bender et al. 1984). However, for natural ecosystems, precise quantitative specification of **A** is rarely possible (Levins 1998).

Instead, under a qualitative approach, only the signs of the aij terms are needed. In traditional "loop analysis," sign specification of **A** alone can provide qualitative predictions of press perturbation impacts (Puccia and Levins 1985), but even in relatively simple systems, multiple feedbacks can result in qualitative predictions with high sign indeterminacy (Dambacher et al. 2003). By using a simulation framework, both parameter uncertainty (i.e., the magnitude of aij) and potential structural uncertainty (i.e., the presence or absence of links) can be incorporated into predictions of community outcomes to a given press perturbation (Melbourne-Thomas et al. 2012, Raymond et al. 2011). As used in the context of QNMs, structural uncertainty refers to instances when it is unclear if a linkage is present or absent, but if it does occur the sign of the link is assumed known (Raymond et al. 2011). The simulation procedure proceeds as follows: (1) a simulated community interaction matrix (**A***) is generated by retaining all certain linkages and the inclusion of uncertain linkages is determined by sampling from a binomial distribution; (2) interaction coefficients (aij) for all links are then sampled from uniform distribution spanning two orders of magnitude (0.01 to 1.0); (3) the simulated community interaction matrix (**A***) is tested against stability criteria (Melbourne-Thomas et al. 2012) and, if the matrix is stable, the negative inverse of **A*** is calculated to obtain the predicted response of the community to a given press perturbation. The procedure is repeated many times (10^4) to obtain distributions of the community outcomes due to a given press perturbation. Further extensions of the simulation approach exist that permit additional filtering of **A*** to only those matrices that also predict community responses in agreement with experimental or observational evidence (Melbourne-Thomas et al. 2012, Raymond et al. 2011).

Model Development

This study sought to build QNMs that described the major ecological interactions likely to influence the dynamics of cultured species and the communities they are embedded within. To do so, a literature review of relevant ecological studies conducted in South Puget Sound and Willapa Bay was conducted and supplemented with studies from other estuaries in the Northeast Pacific. In addition, shellfish growers and researchers with expertise in either system were consulted to identify key cultured bivalves species, their main predators and competitors, and other species or functional groups that, in turn, influence their respective dynamics. Interactions thought to influence the dynamics of variables within the system were identified. Some interactions were considered uncertain, reflecting uncertainty in model structure. Variables included in each QNM are depicted as nodes (Figures 2 and 3) and interactions corresponding with the linkages are described for South Puget Sound and Willapa Bay (Appendix Tables 1 and 2, respectively; p. 52). Further details of model structure are provided for each system as follows.

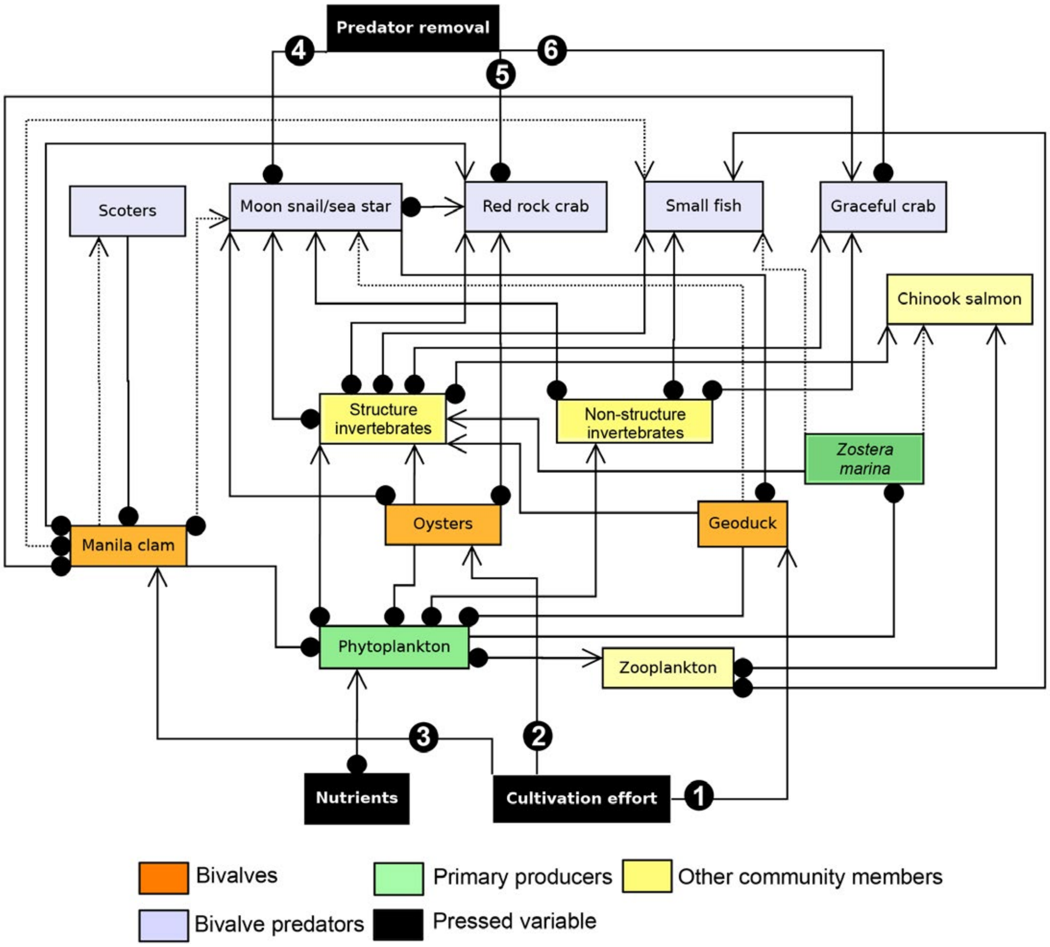


Figure 2. Qualitative interaction network of bivalve aquaculture in South Puget Sound, Washington. Links that terminate with an arrowhead indicate a positive effect; those that terminate with a filled circle indicate a negative effect. Links with both an arrow and a solid circle indicate a predator–prey relationship. All community members have a limiting self-interaction (negative), but for clarity these are not shown. Dashed lines indicate uncertain linkages. Detailed descriptions of the relationships (unnumbered) between nodes are provided in Appendix Table 1. Links labeled 1–6 are included in the model based on the scenario under consideration (see Table 1).

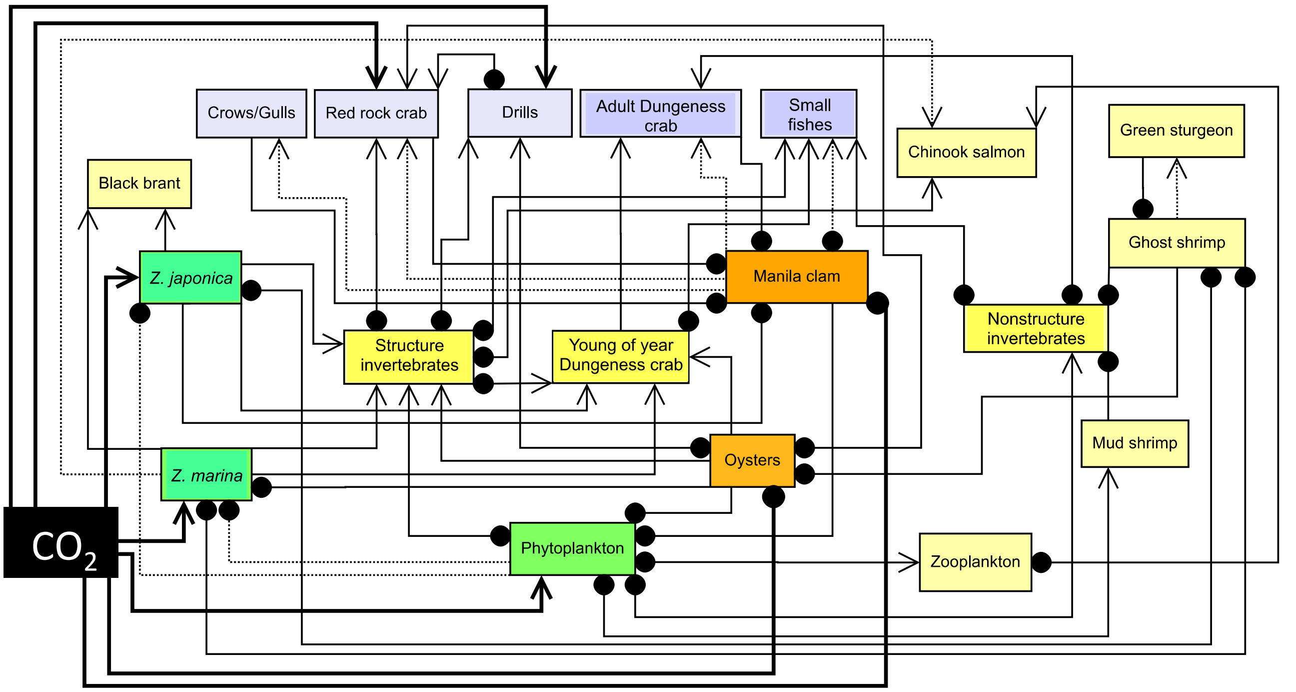


Figure 3. Qualitative interaction network of Willapa Bay, Washington. Lines terminated with arrowheads indicate a positive influence; those terminated with a filled circle indicate a negative influence. Links with both an arrowhead and a solid circle indicate predator–prey relationships. Dashed lines indicate uncertain interactions. Interactions between CO_2 and community members that correspond to different ocean acidification scenarios are in bold. All community members have a limiting (negative) self-interaction, but for clarity these are not shown. Detailed descriptions of the relationships between nodes are provided in Appendix Table 2. See Figure 2 for color legend.

South Puget Sound

For South Puget Sound, the investigators sought to evaluate the potential effects of aquaculture, bivalve predator control, and increased nutrient loadings. Therefore, additional nodes and linkages were included in the QNM to allow simulation of these perturbation scenarios (described under Perturbation Scenarios, p. 40). To simplify the model and reduce the number of nodes, functionally similar species were grouped (Puccia and Levins 1985). For instance, the nodes "small fishes," "zooplankton," and "phytoplankton" represent taxonomically diverse groups, but the ecological function of constituent species was assumed to be similar. In addition, small-bodied benthic invertebrates were grouped into one of two classes: those that associate with structurally complex habitats (e.g., biogenic structure such as eelgrass meadows and oyster beds, as well as growout gear associated with oyster and geoduck cultivation) and those that prefer mud or unstructured habitat (e.g., Ferraro and Cole 2007). The former and latter were referred to as "structure invertebrates" and "non-structure invertebrates," respectively. Although benthic invertebrate community structure may differ among types of complex habitats in South Puget Sound, a simplifying assumption was made that these species play similar functional roles and could be utilized by similar predator assemblages in the absence of detailed information on invertebrate community structure across habitat types.

Willapa Bay

For Willapa Bay, the focus of the modeling was on the potential impacts of OA. Like that used for South Puget Sound, the Willapa Bay QNM also included the main species of cultivated shellfish (Manila clam and Pacific oyster) and ecologically relevant competitors, predators, prey, and other functionally dependent species to capture community interactions. The species included in the model and the nature of their interactions were also informed by a literature review and consultation with shellfish growers and scientists with expertise on the ecology of Willapa Bay. Functionally similar taxa were again grouped to simplify the model in a manner similar to South Puget Sound (e.g., the aggregate variables included "small fishes," "zooplankton," and "phytoplankton"), and small-bodied benthic invertebrates were divided into two functional groups reflecting association with structurally complex (eelgrass beds and oyster beds) and unstructured (mud) habitats (Ferraro and Cole 2007).

Both models are "minimal realistic" in that they include enough detail to capture the interplay of direct and indirect interactions that influence aquaculture and community-wide dynamics but also minimize the number of variables to aid interpretability and reduce prediction uncertainty (Fulton et al. 2003).

Perturbation Scenarios

South Puget Sound

Three main types of perturbation scenarios were considered: (1) increase in bivalve aquaculture, (2) decrease in bivalve predation rates through predator removal, and (3) increase in nutrient loads. To implement the scenarios, the nodes "Cultivation effort" and "Predator removal" were added to the community QNM (Figure 2) and linkages extending from these nodes to community member nodes were added depending on the specific perturbation scenario (Table 1). For example, to evaluate potential community-wide responses to increased geoduck cultivation, a positive link was added to the model, extending from "Cultivation effort" to "Geoduck" (the linkage labeled "1" in Figure 2). The node "Cultivation effort" corresponds to the effort placed by growers into expanding the area over which bivalve cultivation occurs. The remaining labeled linkages (2 through 6) were excluded from the model. The "Cultivation effort" node was then pressed in the simulation, and the response of the community was calculated. Similarly, community responses to increases in Pacific oyster or Manila clam culture were simulated by adding linkages labeled 2 or 3, respectively, to the model, excluding all other labeled linkages, and pressing "Cultivation effort" (Table 1).

In South Puget Sound, anti-predator exclusion technologies (e.g., mesh netting, bag-on-rack or bag-on-bottom methods, protective polyvinyl chloride (PVC) tube sections) are already used extensively on Pacific oyster, Manila clam, and geoduck plots (McDonald et al. 2015, Simenstad and Fresh 1995, Toba et al. 1992); however, predation loss remains an issue. As an added measure, predators could be culled. In practice, this might be achieved by manually removing predators on culture plots or initiating a targeted fishery on predators. The effects of removing predators on the community were evaluated by adding the node "Predator removal," which corresponds to the level of effort applied to bivalve predator removal. The study specifically examined the community-wide effects of removing four common benthic invertebrate predators that were represented by three different nodes in the model: red rock crab *Cancer productus*, graceful crab *Cancer gracilis*, and the moon snail/sea star complex (Figure 2), which is characterized by moon snails (*Euspira lewisii*) and sea stars (sunflower sea star *Pycnopodia helianthoides*, pink sea star *Pisaster brevispinus*, ochre sea star *Pisaster ochraceus*, mottled sea star *Evasterias troscheli*). Negative linkages extending from "Predator removal" to each benthic predator node were added to the model to simulate reductions in predator densities (Table 1).

In the third scenario, an increase in nutrient loadings was considered. In South Puget Sound, nitrogen levels are likely to increase over the next several decades as human populations in the surrounding watersheds grow. In addition, circulation patterns on the Washington coast may shift in response to anthropogenic climate change, resulting in the delivery of additional marine-derived nitrogen relative to present-day conditions (Ahmed et al. 2014, Mackas and Harrison 1997). The effects of a potential future increase in nutrient loadings on the community were evaluated by pressing the node "Nutrients" (Figure 1, Table 1).

In addition to the three main types of perturbation scenarios, the investigators also examined community-wide outcomes when scenarios were combined (Table 1). The goal was to identify how scenario combinations might reinforce or counteract the predicted outcome of community members relative to the individual scenarios.

Table 1. Summary of model scenarios evaluated for the South Puget Sound QNM. For each scenario, the pressed node is indicated (i.e., press variable(s)). Link numbers correspond to labeled links in Figure 2, and the sign of the relationship between the pressed node and community members is denoted. Pressed nodes are as follows: CE, cultivation effort; PR, predator removal; NU, nutrients.

Scenario code	Press	Links added geoduck variable(s)	Pacific oyster	Manila clam	Moon snail/ sea stars	Red rock crab	Graceful crab
A1	CE	1 (+)					
A2	CE		2 (+)				
A3	CE			3 (+)			
A4	CE	1 (+)	2 (+)	3 (+)			
B1	PR				4 (–)		
B2	PR					5 (–)	
B3	PR						6 (–)
B4	PR				4 (–)	5 (–)	6 (–)
C1	NU						
D1	CE, PR	1 (+)	2 (+)	3 (+)	4 (–)	5 (–)	6 (–)
D2	CE, NU	1 (+)	2 (+)	3 (+)			
D3	PR, NU				4 (–)	5 (–)	6 (–)
D4	CE, PR, NU	1 (+)	2 (+)	3 (+)	4 (–)	5 (–)	6 (–)

Willapa Bay

The biological processes that OA can influence at the individual and population levels are likely diverse but are only partially understood. Given this state of knowledge, the intention of this study was not to evaluate all OA effects but rather explore the potential role of community interactions in mediating and propagating three commonly discussed OA impacts, as follows:

- OA will stimulate primary production. Increased pCO_2 can cause a fertilization effect that elevates photosynthetic rates, leading to higher growth rates among phytoplankon and eelgrass (Koch et al. 2013, Kroeker et al. 2013, Palacios and Zimmerman 2007, Thom 1996, Zimmerman et al. 1997).
- OA will decrease bivalve production. OA may reduce bivalve production directly by reducing larval survival or adversely affecting variables that influence survival like individual growth, development, and calcification rates (Barton et al. 2012, Kurihara et al. 2007, Timmins-Schiffman et al. 2012, Waldbusser et al. 2013). These effects in turn may reduce the density or viability of natural or outplanted sets (Barton et al. 2012).
- OA will alter predator–prey interaction strengths. OA may cause declines in bivalve shell strength, thickness, or size, resulting in higher vulnerability to predators, thereby strengthening predation interactions (Kroeker et al. 2014, Sanford et al. 2014).

The qualitative network model included the variable "CO_2," which represents carbonate chemistry conditions (Figure 3). It was linked to species in a manner that corresponded to different hypothesized OA effects (Figure 3). First, model scenarios were examined in which the effect of CO_2 was linked to individual functional groups or species of primary producers (phytoplankton; the eelgrasses *Z. marina* and *Z. japonica*) and another in which CO_2 affected all primary producers simultaneously (Table 2). Next, the effect of CO_2 was linked to individual bivalve species (Pacific oyster, Manila clam) and to both species simultaneously (Table 1). Finally, the potential for enhanced predatory interactions was tested at two points in the model: the predation linkages between red rock crab (predator) and Pacific oysters (prey) and between drills (predatory gastropods) and Pacific oysters (prey). To simulate enhanced predation due to OA, positive interactions extending from CO_2 to the predator and negative interactions extending from CO_2 to the prey were added (Dambacher and Ramos-Jiliberto 2007). Model scenarios were examined where enhanced interactions were considered individually and in combination (Table 1). In addition to the three main scenarios, the study evaluated community responses in scenarios that included pair-wise combinations of the three hypotheses as well as a scenario that included all hypothesized OA effects acting simultaneously (Table 1).

Simulations

A simulation approach was used to estimate the level of sign determinacy in the predicted response of community members to the different press scenarios (Melbourne-Thomas et al. 2012, Raymond et al. 2011). The following simulation protocol was used: (1) a community matrix configuration was first generated by sampling uncertain links from a binomial distribution, (2) the interaction strengths of the community matrix were then drawn from a uniform distribution that spanned two orders of magnitude (0.01 to 1), and all negative self-effect interaction coefficients were drawn from a uniform distribution spanning 0.25 to 1 (Raymond et al. 2011), and (3) the community matrix was checked against system stability criteria (Melbourne-Thomas et al. 2012) and, if stable, the responses of the community to the press perturbation were calculated. If unstable, the community matrix was discarded and a new community matrix was drawn and the simulation procedure was run again. For each scenario, the sign responses from 104 stable community matrices were obtained.

Table 2. Summary of the OA scenarios examined using QNMs of ecological interactions in Willapa Bay, Washington. For each scenario, the qualitative relationship (sign) linking the variable CO_2 to the respective community member is listed in the table column.

		Primary producers			**Bivalves**		**Enhanced drill–oyster predator interaction**		**Enhanced red rock crab–oyster predator interaction**	
Scenario	Scenario code	Phyto	*Z. marina*	*Z. japonica*	Pacific oyster	Manila clam	Drills	Pacific oyster	Red rock crab	Pacific oyster
Primary	A1	(+)								
producer	A2		(+)							
	A3			(+)						
	A4		(+)	(+)						
	A5	(+)	(+)	(+)						
Bivalves	B1				(–)					
	B2					(–)				
	B3				(–)	(–)				
Enhanced	C1						(+)	(–)		
predation	C2								(+)	(–)
	C3						(+)	(–)	(+)	(–)
Combinations	D1 (A5+B3)	(+)	(+)	(+)	(–)	(–)				
	D2 (A5+C3)	(+)	(+)	(+)			(+)	(–)	(+)	(–)
	D3 (B3+C3)				(–)	(–)	(+)	(–)	(+)	(–)
	D4 (A5+B3+C3)	(+)	(+)	(+)	(–)	(–)	(+)	(–)	(+)	(–)

Linkage Influence

In addition to yielding predictions, QNMs can also be analyzed to gain insight into which linkages principally influence the sign outcome of community members to a given press scenario (Melbourne-Thomas et al. 2012). To illustrate the method, an assessment was made of the linkage influence on Willapa Bay community responses to the press scenario in which all hypothesized OA linkages were included (scenario D4, Table 2).

To simplify analysis, no structural uncertainty in the model was assumed (Raymond et al. 2011). That is, all linkages, including those noted as uncertain, were retained in the network. Next, 1,500 community matrices were simulated and their associated press perturbation response to OA calculated. For each community member, investigators fit a multivariate adaptive regression splines (MARS) model in which the simulated interaction coefficient parameters were treated as predictor variables and the sign outcomes of species to the press perturbation were the response variables. MARS are a nonparametric statistical method that can fit nonlinear functions and higher-order interactions (Friedman 1991, Hastie et al. 2009). The method is well suited for analyzing large datasets and combines the strengths of regression trees and spline fitting by replacing the step functions normally associated with regression trees with piecewise linear basis functions (Hastie et al. 2009). In an earlier study, Boosted Regression Trees (BRT) models were introduced as tools for evaluating linkage influence on node responses in QNMs (Melbourne-Thomas et al. 2012). The BRT approach also permits estimation of nonlinear responses and higher-order interactions and, in some cases, performance based on predictive ability is comparable with or slightly better than MARS (Elith et al. 2006, Stohlgren et al. 2010). However, the MARS algorithm enabled variable selection based on deviance reduction criteria, which was useful for identifying subsets of key linkages. Furthermore, in preliminary comparisons, MARS was computationally faster than BRT, which was valuable given the intended number of models to fit.

The MARS models were fit assuming a binomial response error model following Leathwick et al. (2005). Variables were retained if they reduced the residual squared error of the model by 0.01 or more. For all fitted models, the percentage of explained deviance associated with each retained predictor (i.e., the predictor's relative importance) was calculated (Milborrow 2014). Cluster analyses were performed on the relative importance values to identify both linkages that influenced similar community members and community members that were influenced by similar linkages; dendrograms were calculated based on the Bray–Curtis dissimilarity coefficient and the complete linkage clustering method (Legendre and Legendre 1998). All statistical analyses were performed using the statistical software package "R" version 3.0.3 (R Development Core Team 2014). MARS models were estimated using the library "earth" version 4.0.0 (Milborrow 2014) and dendrograms were calculated using the library "vegan" version 2.0-10 (Oksanen et al. 2013).

RESULTS

South Puget Sound

Cultivation Effort

Increased cultivation effort, when applied to individual bivalve species (scenarios A1 through A3), resulted in positive responses to the bivalve species directly affected. Sign determinacy, which corresponds to the level of consistency in the simulated sign responses, was greater than 70% in all scenarios (Figure 4). For most other community members, sign determinacy was lower (less than 70%) but some trends were apparent. Phytoplankton responded negatively and *Z. marina* responded positively across scenarios, and the bivalve predator red rock crab increased as well (Figure 4). Consistent trends in other community members toward negative (zooplankton, non-structure invertebrates) and positive responses (nutrients) were also observed (Figure 4).

In contrast, when cultivation effort was applied to all three bivalve species simultaneously (scenario A4), each bivalve species responded positively but sign determinacy decreased relative to the individual press scenarios for Manila clam and Pacific oyster relative to their individual press scenarios (Figure 4). Additionally, the sign responses for nutrients, phytoplankton, zooplankton, non-structure invertebrates, *Z. marina*, and red rock crab were similar to those under the individual scenarios, but for these community members sign determinacy increased, exceeding 70% (Figure 4).

Predator Removal

In the individual predator removal scenarios (B1 to B3), each targeted predator decreased (Figure 4). However, the responses of cultured bivalve populations to the different predator removal scenarios varied. Removing moon snails/sea stars (B1) increased geoduck and Pacific oyster populations, while removing red rock crabs (B2) increased Manila clams but decreased geoduck populations. Removing graceful crab (B3) also increased Manila clams, but Pacific oyster populations decreased. Responses of the remaining community members also differed as well between scenarios, with no consistent trends in sign responses among primary producers, bivalve predators, or other community members (Figure 4).

In the scenario in which all three predators were removed simultaneously (scenario B4), the sign responses of the predators were negative, sign determinacy was low, and among the cultured bivalves, only Manila clam population numbers showed a positive response with high sign determinacy (Figure 4). Primary producers, nutrients, and zooplankton responded in the same manner as when cultivation effort was increased on all three species simultaneously (Figure 4).

Nutrients

For primary producers, increased nutrients resulted in a positive response in phytoplankton and negative response in *Z. marina* (scenario C1), which was the opposite of the pattern observed in the cultivation effort and predator control scenarios

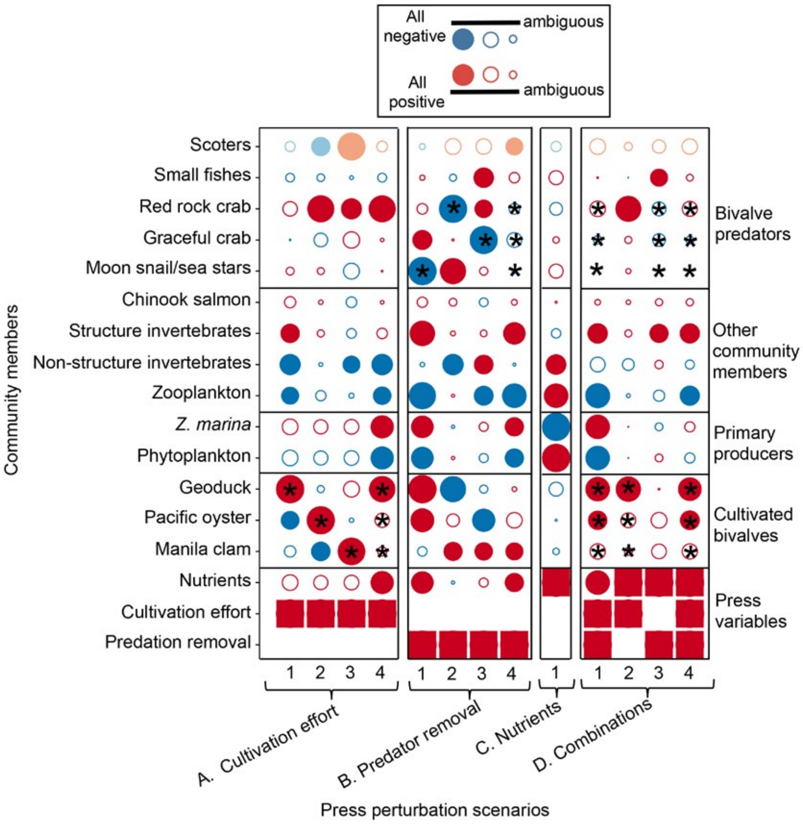


Figure 4. Simulated community responses to increased bivalve cultivation effort, benthic predator removals, and nutrients inputs in South Puget Sound, Washington. Scenario letter and number codes correspond to scenario descriptions provided in Table 1. Nodes pressed in each scenario are indicated by a solid square. The relative size of the red and blue circles scale with the level of consistency of the simulated sign response of community members. For added reference, solid circles indicate sign consistency greater than 70%; open circles indicate less than or equal to 70%. Red and blue symbol colors correspond to net positive and negative responses, respectively. Light red and light blue symbols indicate instances where greater than 25% of the simulated responses were 0 (symbol scale is based on the non-zero predicted sign responses). For each scenario, community members directly linked to the pressed variable(s) are noted by an asterisk overlying their respective responses.

(Figure 4). Further, increased nutrients resulted in a predicted increase in phytoplankton and non-structure invertebrates (Figure 4). Responses for all the remaining community members, including the bivalves and bivalve predators, had low sign determinacy (Figure 4).

Scenario Combinations

In scenario D1, cultivation effort and predator removals for all three bivalves were pressed. Overall, the sign responses of all bivalves, primary producers, nutrients, and zooplankton were similar to both separate scenarios (A4 and B4), though variation in sign determinacy was apparent for a few community members (e.g., red rock crab, structure invertebrates, Pacific oyster, manila clam; Figure 4).

With increased nutrients and cultivation effort (scenario D2), most community members exhibited responses with low sign determinacy; only geoduck and red rock crab (both positive responses) showed high sign determinacy. Similarly, sign determinacy was predominately low for community members when nutrients and predator removal were increased (D3). In that case, positive responses in small fishes and structure invertebrates had high sign determinacy.

Last, simultaneous increases in cultivation effort, predator removal, and nutrients (scenario D4) resulted in positive responses in all three bivalves, though sign determinacy was high for only geoduck and Pacific oyster (Figure 4). As for the remaining community members, only two exhibited responses with high sign determinacy — structure invertebrates and zooplankton — which responded positively and negatively, respectively (Figure 4).

Willapa Bay

Community Responses Across OA Scenarios

In general, the level of sign determinacy exceeded 70% for 21–57% of the community members regardless of the OA scenario (Figure 5). For several community members, including phytoplankton, Manila clam, mud shrimp, and crows/gulls, sign determinacy was high across most OA scenarios and the sign of the response was also consistent (Figure 5). In contrast, sign determinacy was low in the responses of other community members (e.g., small fishes, non-structure invertebrates, adult Dungeness crab) regardless of the OA scenario (Figure 5).

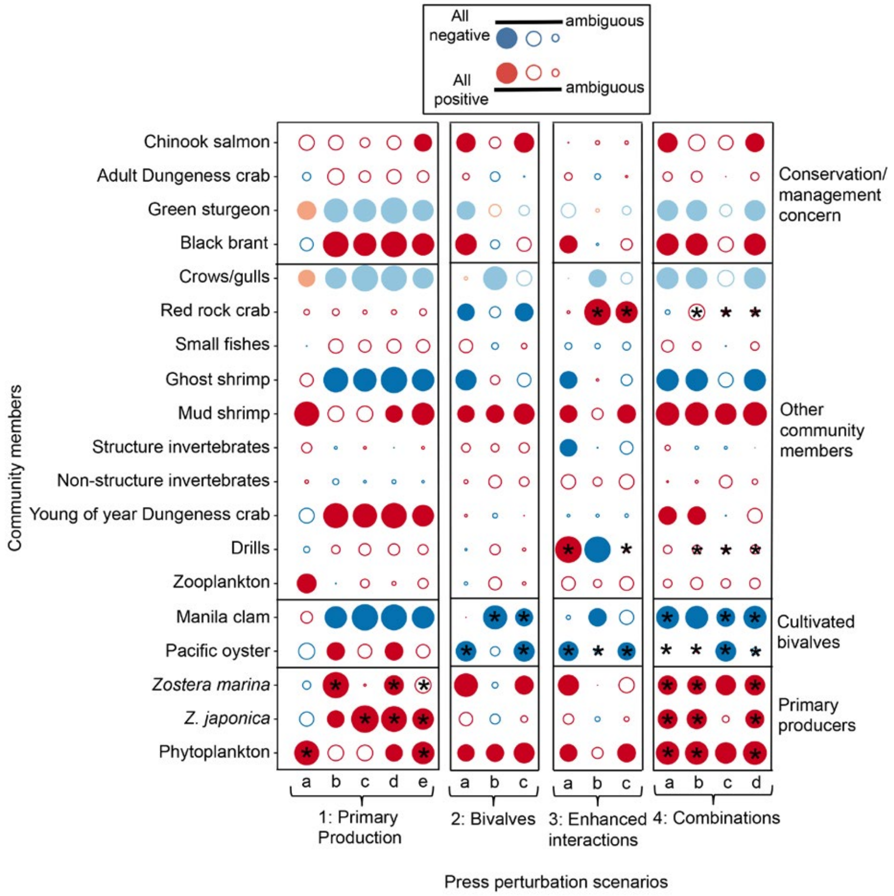


Figure 5. Simulated community responses to increased CO_2 in Willapa Bay, Washington. Scenario letter and number codes correspond to scenario descriptions provided in Table 2. The relative size of the circle symbols scale with the level of consistency of the simulated sign response of community members. For added reference, closed circles indicate sign consistency greater than 70%; open circles indicate less than or equal to 70%. Red and blue symbol colors correspond to net positive and negative responses, respectively. Light red and light blue symbols indicate instances where greater than 25% of the simulated responses were 0 (symbol scale is based on the non-zero predicted sign responses). For each scenario, community members directly linked to CO_2 are noted by an asterisk overlying their respective responses.

Primary Producers

In the primary producer scenarios in which phytoplankton, *Z. marina*, and *Z. japonica* were linked directly with CO_2 (scenarios 1a–c), the linked species exhibited positive responses in their respective scenarios (Figure 5). However, in scenario 1b, the direct effect of CO_2 on *Z. marina* was also associated with an increase in *Z. japonica* via indirect pathways. Similarly, in scenario 1d where more than one community member was linked to CO_2, indirect pathways resulted in a positive response in phytoplankton when direct effects of CO_2 were included for *Z. japonica* and *Z. marina*. In contrast, direct linkages with CO_2 did not correspond to high sign determinacy in the response of *Z. marina* when all three primary producers were linked to CO_2 (scenario 1e, Figure 5).

Among species of conservation or management concern, results were mixed. The response of the herbivorous black brant was consistently positive in all scenarios that included direct linkages between CO_2 and either eelgrass species (Figure 5). However, the response of the threatened green sturgeon was negative but unclear owing to model structural uncertainty (Figure 5). While the response of adult Dungeness crab was ambiguous across all primary producer scenarios, the response of Chinook salmon was unambiguous and positive only when direct positive CO_2 effects were included for all primary producers (scenario 1e, Figure 5). Ghost shrimp, which can destabilize the substrate and smother oysters with sediments, responded negatively in all scenarios in which eelgrass increased, as did crows/gulls though uncertainty due to model structure was high (Figure 5).

Bivalves

In the bivalve scenarios (2a–c), direct negative linkages between CO_2 and Pacific oyster and Manila clam were associated with reductions in both species (Figure 5). However, in terms of indirect effects, the number of community members affected by reductions in both species differed. A decrease in Pacific oyster (scenario 2a) was associated with likely changes in eight community members, while responses were more ambiguous in the Manila clam scenario (2b), with likely change predicted in only three members (Figure 5). Across bivalve scenarios, all showed a positive increase in phytoplankton, while increases in the eelgrass *Z. marina* were observed only in Pacific oyster scenarios (2a and c, Figure 5). Several of the remaining community members also differed in level of sign determinacy between the three bivalve scenarios (Figure 5).

Enhanced Predation Interaction

Overall, the response of the community to enhanced predation on Pacific oyster differed depending on which predation interaction was enhanced. Increased predation by drills (3a) resulted in community responses similar to those observed in bivalve scenario 2a, except for a negative response in structure invertebrates, a positive response in drills, and higher ambiguity in the response of Chinook salmon, green sturgeon, and red rock crab (Figure 5). In contrast, the community response to enhanced red rock crab predation differed substantially; relative to scenario 2a, the responses of several community members increased in ambiguity, including the response of Pacific oyster, and negative responses were predicted for drills, Manila clam, and crows/gulls (Figure 2). When both predatory interactions (drills–Pacific oyster and red rock crab–Pacific oyster) were enhanced (scenario 3c), ambiguity increased further in the response of drills relative to scenario 3b, where only the drill–Pacific oyster interaction was enhanced, and ambiguity in the sign response of most community members remained high (Figure 2).

In general, community responses in scenarios that included linkage combinations from the three different sets of OA hypotheses were relatively consistent when direct linkages from CO_2 to the three primary producers were included (scenarios 4a, b, and d, Figure 2). Only the level of ambiguity in the responses of Chinook salmon and young of year Dungeness crab differed among the scenarios (Figure 2). Conversely, negative direct effects on bivalves and enhanced predation by red rock crab and drills on Pacific oyster yielded community responses with higher levels of ambiguity relative to the other scenarios (scenario 4c, Figure 2). Furthermore, in all scenarios, sign ambiguity in the outcomes of Pacific oyster, drills, and red rock crab remained high even though each species was connected to CO_2 through direct linkages (Figure 2).

Linkage Influence

Linkages with interaction strengths that were associated with the sign response of community members to OA were determined (Table 3). For all species, the proportion of positive responses from the simulated community interaction matrices ranged from 0.19 to 0.93, with an average of value of 0.56 (Table 3). The proportion of deviance in the sign responses of community members explained by the MARS models was variable, ranging from 7% to 42% (Table 3). Of the 7 direct linkages between CO_2 and various community members in the OA scenario, 1 to 4 linkages (average: 2.8) were included as important predictors of sign responses; of the 70 non-CO_2 linkages, between 4 and 14 linkages (average: 8.7) were also included as predictors (Table 3).

Linkages between CO_2 and phytoplankton, *Z. japonica*, *Z. marina*, Pacific oyster, and Manila clam were important to varying degrees in predicting sign responses in 16, 13, 11, 9, and 6 community members, respectively (Figure 6). However, direct linkages between CO_2 and red rock crab and drills were not important in modeling variance in the response of any community member.

Table 3. Summary of multivariate adaptive regression splines (MARS) models predicting the sign response of Willapa Bay community members where community interaction coefficients are predictor variables. For each MARS model, the count of OA and non-OA linkages included in the fitted model are noted. The total potential number of OA and non-OA linkages are 6 and 70, respectively. Asterisks (*) denote species with direct linkages to CO_2 in the press scenario.

Community member	Proportion (–)	% deviance explained	OA linkages	Non-OA linkages
*Zostera japonica**	0.28	42	2	9
Ghost shrimp	0.81	35	3	9
Green sturgeon	0.81	35	3	9
Black brant	0.19	31	4	10
Pacific oyster*	0.66	30	4	13
Young of year Dungeness crab	0.27	29	4	12
Crows/gulls	0.84	24	4	6
Manila clam*	0.84	24	4	6
*Z. marina**	0.19	25	3	4
Zooplankton	0.45	23	2	11
Non-structure invertebrates	0.39	20	1	9
Structure invertebrates	0.38	19	2	14
Small fishes	0.37	17	4	12
Adult Dungeness crab	0.46	17	4	10
Drills*	0.28	15	4	9
Mud shrimp	0.07	12	1	5
Phytoplankton*	0.07	12	1	5
Red rock crab*	0.78	12	2	9
Chinook salmon	0.11	7	3	4

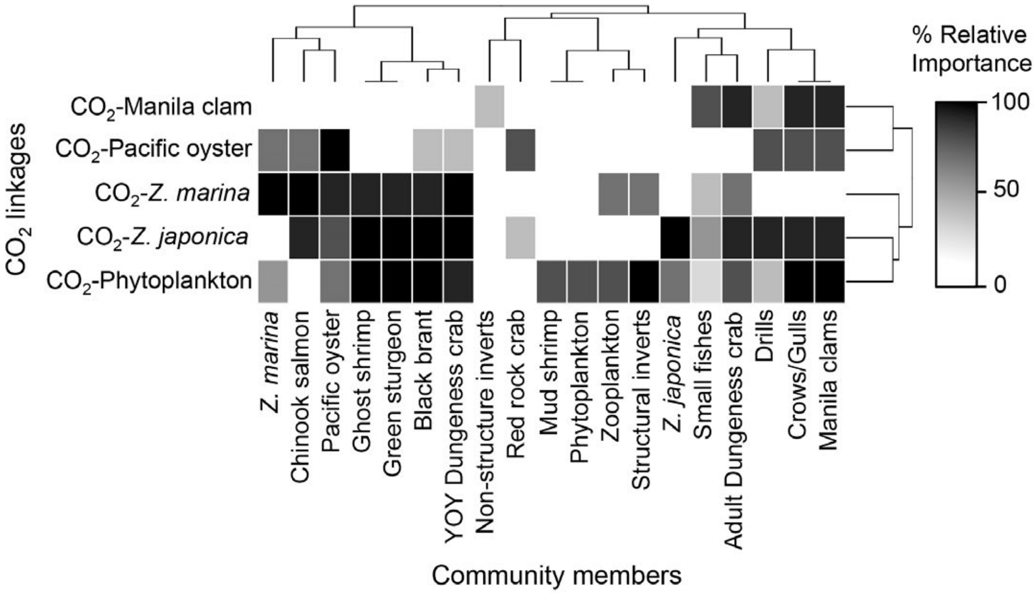


Figure 6. Relative importance of the interaction strength of direct CO$_2$ linkages to the sign response of community members to a CO$_2$ press perturbation. Community members and linkages are both ordered according to similarity.

Partial dependency plots were examined for Pacific oyster, which had an ambiguous sign response to the press scenario (63% of responses were negative, Table 3). In total, 14 linkages were included in the Pacific oyster MARS model, but for brevity and illustrative purposes, partial dependency plots were presented for the five most important linkages in terms of deviance reduction; these linkages account for ~70% of the explained deviance and include three linkages to CO$_2$ and two non-CO$_2$ linkages (Figure 7a–f). As expected, the probability of a negative response in Pacific oyster increased with the strength of the negative CO$_2$–Pacific oyster interaction (Figure 7a). However, the probability decreased as interaction strength between CO$_2$ and *Z. marina* and *Z. japonica* increased (Figure 7b–c). Among the non-CO$_2$ interactions, negative responses were more likely when the negative *Z. marina*–ghost shrimp and ghost shrimp–Pacific oyster interactions were weak, and less likely when the negative phytoplankton–*Z. marina* interaction was weak (Figure 7d–e).

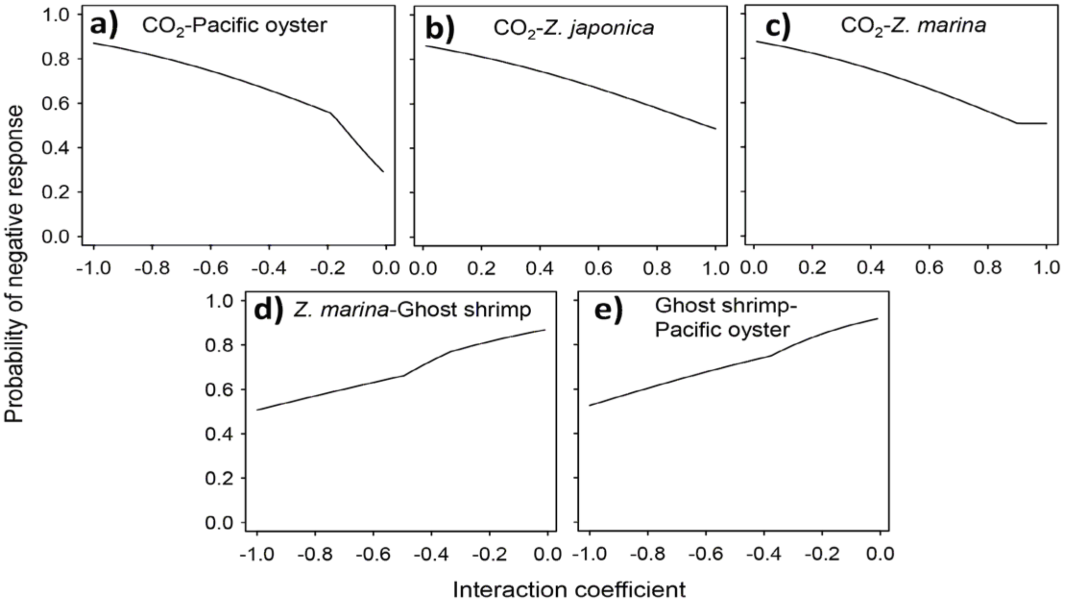


Figure 7. Partial dependence plots of the sign response of Pacific oyster to the five most important interaction coefficients in the community matrix.

DISCUSSION

As shown for South Puget Sound and Willapa Bay, specifying network structure alone can allow qualitative prediction and help identify outcomes that may be counterintuitive or potential tradeoffs resulting from a particular management or environmental change scenario. For instance, in the individual scenarios for bivalve cultivation effort, tradeoffs between different bivalve species were predicted: cultivation effort applied to geoduck alone increased geoduck, but led to decreases in Pacific oyster. Similarly, cultivation effort applied only to Pacific oyster increased Pacific oyster, but led to a decrease in Manila clam. Such patterns are likely due in part to indirect pathways involving the predator red rock crab, wherein an increase in one bivalve results in higher abundances of red rock crab, which increases predation on other bivalve prey. Tradeoffs were also evident in removal scenarios of individual predators, which had opposing effects on different bivalve species: removing red rock crab decreased geoduck and increased Manila clam, while removing graceful crab decreased Pacific oyster and increased Manila clam. Because QNMs integrate direct effects, indirect effects, and feedbacks, they can help identify tradeoffs arising from complex ecological interactions that might otherwise be difficult to anticipate (Levins 1998).

A key benefit of QNMs is that they allow rapid assessment of many scenarios and can help screen management actions that may yield ambiguous or problematic outcomes (Carey et al. 2014, Dambacher et al. 2009). For example, increased cultivation effort in the South Puget Sound QNM did not always ensure increased bivalve production. In scenarios where cultivation effort was applied to only one species of bivalve, the species responded positively and with high sign determinacy. However, under the multispecies press scenario, sign determinacy of the response of two of the three bivalves (Pacific oyster and Manila clam) decreased relative to the individual species press scenarios. Combining cultivation effort with predator removals or increased nutrients also resulted in ambiguous responses in some bivalves. The reduced sign determinacy is due to increases in the number of countervailing feedbacks; that is, the number of pathways conveying negative effects increased relative to the number conveying positive effects (Dambacher et al. 2003). Sign determinacy could be improved with quantitative information on interaction strengths, but this may be impractical to obtain (Dambacher et al. 2003, Puccia and Levins 1985). From a precautionary perspective, analyzing a variety of development and management scenarios can offer insight into conditions that lead to increased outcome uncertainty and into where action should proceed with caution (Carey et al. 2014).

For complicated QNMs, statistical analyses of associations between the simulated interaction coefficients and the predicted response of species provide a simple approach for revealing key linkages and the manner in which they influence the likelihood of negative or positive outcomes. For instance, under the scenario in which all hypothesized OA effects occur in Willapa Bay (scenario 4d), the sign response of Pacific oyster was ambiguous, but analysis of the simulated responses using MARS showed that the sign depended on the magnitude of a subset of network interactions. Unsurprisingly, the probability of observing a negative response in Pacific oyster increased with the negative interaction strength between CO_2 and Pacific oyster. However, the remaining linkages indicate that the effect of CO_2 on eelgrasses is transmitted to Pacific oyster indirectly through a linkage to ghost shrimp. Ghost shrimp negatively influence Pacific oysters and a decline in ghost shrimp due to an increase in eelgrass (via their negative interaction) decreases the probability of observing a negative response in Pacific oyster. Whether the interaction pathway is able to counteract the direct negative effects of OA on Pacific oysters will require additional study and highlights an area on which to focus future research. In the same vein, systematic assessment of linkage influence for all community members can highlight important community-wide interactions. Among the hypothesized direct CO_2 effects in Willapa Bay, the CO_2–phytoplankton interaction was retained as a significant predictor for a majority of community members (84%), while the CO_2–Manila clam linkage influenced the fewest (31%). Such information can help identify research priorities when considering the community as a whole.

The scenarios examined for South Puget Sound aquaculture reflect a small subset of potential applications, and the models could easily be tailored to address other aquaculture management issues including pest eradication, invasive species, disease, and climate variability. In addition, changes in policy that influence aquaculture permitting practices could also be evaluated using the QNM. For instance, it was assumed that aquaculture would not expand into eelgrass habitats in South Puget Sound, in accordance with current regulations. A policy change allowing aquaculture expansion into eelgrass could be simulated by adding negative linkages to *Z. marina* from the bivalve species that are cultivated at the same tidal depths where *Z. marina* occurs (e.g., Pacific oyster and geoduck; Ruesink and Rowell 2012, Tallis et al. 2009, Wagner et al. 2012). In the network corresponding to such a policy change, an increase in either bivalve species would have a negative effect on *Z. marina*. More generally, the network could be expanded further to include social and economic variables (e.g., demand, profit, jobs, recreational opportunities, scenic quality) to examine social–ecological tradeoffs in support of more holistic management approaches (Cranford et al. 2012, Dambacher et al. 2009, Soto et al. 2008).

Similar to other modeling approaches, QNMs have important limitations. First, a key assumption underpinning the method is that system variables are at or near equilibrium or closely tracking moving equilibrium conditions (Puccia and Levins 1985). In marine ecosystems, frequent disturbances (e.g., climate variability, pollution, fishing) may make this assumption unrealistic (Dambacher et al. 2009). However, the assumption is also routinely used in quantitative community and food web models (Bender et al. 1984, Yodzis 1998) and, if the system exhibits sustained bounded motion, the issue can be addressed by considering predicted responses within the context of an appropriately long time scale (Dambacher et al. 2009, Puccia and Levins 1985).

Second, the model assumes that the partial derivatives of system variables are adequately approximated by linear functions near equilibrium conditions. Strong nonlinearity may result from the system transitioning across a threshold, whereby links may be created or broken, or reversed in sign. Such thresholds would require the consideration of multiple networks corresponding to different states of the system (Dambacher and Ramos-Jiliberto 2007). Last, like all ecosystem models, simplifying assumptions were made regarding how species were aggregated. In general, an effort was made to aggregate sets of species into variables that would likely possess similar linkages and therefore respond similarly to system perturbations (Puccia and Levins 1985). The necessity of lumping variables in speciose ecosystems and the associated caveats of doing so are understood well in both qualitative and quantitative ecosystem modeling arenas (Fulton et al. 2003, Metcalf et al. 2008), and the final models reflected study efforts to simplify these estuarine food webs to improve interpretability.

Although quantitative models are helpful for understanding and predicting the effects of aquaculture, they are difficult to parameterize in systems with limited data. Qualitative models offer an alternative method, requiring as a minimum only basic knowledge of the natural history of key species composing a system (Levins 1998). QNMs provide imprecise predictions, but this can be viewed as advantageous because emphasis is moved away from the precise measurement of parameters (which may be costly and difficult or impossible to do) and towards understanding the main processes and community interactions that influence the dynamics of the complete system (Dambacher et al. 2009, Puccia and Levins 1985). Ecosystem approaches to aquaculture require modeling methods that can synthesize systems-level processes. QNMs are flexible, highly robust, and effective frameworks for organizing diverse types of information, and they should be of considerable value to resource managers and growers alike.

ACKNOWLEDGMENTS

We thank Brett Dumbauld, Jennifer Ruesink, Jameal Samhouri, Latitia Conway-Cranos, Erin Graham, and Terrie Klinger for helpful comments on earlier versions of this manuscript. We also thank participants from our August 2014 workshop facilitated by Washington Sea Grant on the ecology and economics of shellfish aquaculture in Washington State.

This report is a synthesis of two journal articles published in October 2015:

Reum JCP, Ferriss BE, McDonald PS, Farrell DM, Harvey CJ, Klinger T, Levin PS (2015) Evaluating community impacts of ocean acidification using qualitative network models. Marine Ecology Progress Series 536:11-24. doi: 10.3354/meps11417.

Reum JCP, McDonald PS, Ferriss BE, Farrell DM, Harvey CJ, Levin PS (2015) Qualitative network models in support of ecosystem approaches to bivalve aquaculture. ICES Journal of Marine Science. doi: 10.1093/icesjms/fsv119.

LITERATURE CITED

Ahmed A, Pelletier G, Robers M, Kolosseus A (2014) South Puget Sound dissolved oxygen study: water quality model calibration and scenarios. Washington Department of Ecology, Olympia, Washington, 158 p.

Banas N, Hickey B, Newton J, Ruesink J (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecology Progress Series 341:123–139.

Barton A, Hales B, Waldbusser GG, Langdon C, Feely RA (2012) The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. Limnology and Oceanography 57:698–710.

Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. Ecology 65:1–13.

Borges AV, Abril G (2011) Carbon dioxide and methane dynamics in estuaries. In McClusky D, Wolanski E (eds) Treatise on Estuarine and Coastal Science, Vol 5. Waltham: Academic Press, pp. 119–161.

Burns R (1985) The shape and form of Puget Sound. Washington Sea Grant Program, Seattle, Washington, 100 p.

Byron C, Link J, Costa-Pierce B, Bengtson D (2011) Calculating ecological carrying capacity of shellfish aquaculture using mass-balance modeling: Narragansett Bay, Rhode Island. Ecological Modelling 222:1743–1755.

Carey MP, Levin PS, Townsend H, et al. (2014) Characterizing coastal foodwebs with qualitative links to bridge the gap between the theory and the practice of ecosystem-based management. ICES Journal of Marine Science 71:713–724.

Castillo GC, Li HW, Rossignol PA (2000) Absence of overall feedback in a benthic estuarine community: a system potentially buffered from impacts of biological invasions. Estuaries 23:275–291.

Cranford PJ, Kamermans P, Krause G, et al. (2012) An ecosystem-based approach and management framework for the integrated evaluation of bivalve aquaculture impacts. Aquaculture Environment Interactions 2:193–213.

Dambacher JM, Brewer DT, Dennis DM, Macintyre M, Foale S (2007) Qualitative modelling of gold mine impacts on Lihir Island's socioeconomic system and reef-edge fish community. Environmental Science & Technology 41:555–562.

Dambacher JM, Gaughan DJ, Rochet MJ, Rossignol PA, Trenkel VM (2009) Qualitative modelling and indicators of exploited ecosystems. Fish and Fisheries 10:305–322.

Dambacher JM, Li HW, Rossignol PA (2003) Qualitative predictions in model ecosystems. Ecological Modelling 161:79–93.

Dambacher JM, Ramos-Jiliberto R (2007) Understanding and predicting effects of modified interactions through a qualitative analysis of community structure. The Quarterly Review of Biology 82:227–250.

Dambacher JM, Young JW, Olson RJ, et al. (2010) Analyzing pelagic food webs leading to top predators in the Pacific Ocean: a graph–theoretic approach. Progress in Oceanography 86:152–165.

Duarte CM, Hendricks IE, Moore TS, et al. (2013) Is ocean acidification an open-ocean syndrome? Understanding anthropogenic impacts on seawater pH. Estuaries and Coasts 36(2):221–236.

Elith J, Graham CH, Anderson RP, et al. (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Feldman KL, Armstrong DA, Dumbauld BR, DeWitt TH, Doty DC (2000) Oysters, crabs, and burrowing shrimp: review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. Estuaries 23:141–176.

Feely RA, Sabine CL, Hernandez-Ayon M, Ianson D, Hales B (2008) Evidence for upwelling of corrosive 'acidified' water onto the continental shelf. Science 320:1490-1492.

Ferraro SP, Cole FA (2007) Benthic macrofauna–habitat associations in Willapa Bay, Washington, USA. Estuarine, Coastal and Shelf Science 71:491–507.

Ferriss B, Reum JCP, Farrell D, McDonald PS, Harvey C (2015) A quantitative approach to understanding potential trophic and non-trophic interactions between shellfish aquaculture and the Central Puget Sound food web. In Ecology and Economics of Shellfish Aquaculture in Washington State. Washington Sea Grant, Seattle.

Friedman JH (1991) Multivariate adaptive regression splines. The Annals of Statistics 19:1–67.

Fulton EA, Smith AD, Johnson CR (2003) Effect of complexity on marine ecosystem models. Marine Ecology Progress Series 253:1–16.

Harvey C, Williams G, Levin P (2012) Food web structure and trophic control in Central Puget Sound. Estuaries and Coasts 35:821–838.

Hastie T, Tibshirani R, Friedman J, Hastie T, Friedman J, Tibshirani R (2009) The Elements of Statistical Learning. Springer, New York, 745 p.

Hickey BM, Banas NS (2003) Oceanography of the US Pacific Northwest Coastal Ocean and estuaries with application to coastal ecology. Estuaries 26:1010–1031.

Jiang W, Gibbs MT (2005) Predicting the carrying capacity of bivalve shellfish culture using a steady, linear food web model. Aquaculture 244:171–185.

Koch M, Bowes G, Ross C, Zhang XH (2013) Climate change and ocean acidification effects on seagrasses and marine macroalgae. Global Change Biology 19:103–132.

Kroeker KJ, Micheli F, Gambi MC (2013) Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. Global Change Biology 19(6):1884–1896.

Kroeker KJ, Sanford E, Jellison BM, Gaylord B (2014) Predicting the effects of ocean acidification on predator–prey interactions: a conceptual framework based on coastal molluscs. The Biological Bulletin 226:211–222.

Kurihara H, Kato S, Ishimatsu A (2007) Effects of increased seawater pCO_2 on early development of the oyster *Crassostrea gigas*. Aquatic Biology 1:91–98.

Lane P, Levins R (1977) The dynamics of aquatic systems. 2. The effects of nutrient enrichment on model plankton communities. Limnology Oceanography 22:454–471.

Leathwick JR, Rowe D, Richardson J, Elith J, Hastie T (2005) Using multivariate adaptive regression splines to predict the distributions of New Zealand's freshwater diadromous fish. Freshwater Biology 50:2034–2052.

Legendre P, Legendre L (1998) Numerical Ecology, 2nd ed. Elsevier Science, Amsterdam, 852 p.

Levins R (1974) The qualitative analysis of partially specified systems. Annals of the New York Academy of Sciences 231:123–138.

Levins R (1998) Qualitative mathematics for understanding, prediction, and intervention in complex ecosystems. In Raport D, Costanza R, Epstein P, Gaudet C, Levins R (eds) Ecosystem Health. Blackwell Science, MA, pp. 178–204.

Mackas DL, Harrison PJ (1997) Nitrogenous nutrient sources and sinks in the Juan de Fuca Strait/Strait of Georgia/Puget Sound Estuarine System: assessing the potential for eutrophication. Estuarine, Coastal and Shelf Science 44:1–21.

McDonald P, Galloway AW, McPeek KC, VanBlaricom GR (2015) Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington, USA. Journal of Shellfish Research 34:189–202.

McKindsey CW, Thetmeyer H, Landry T, Silvert W (2006) Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261:451–462.

Melbourne-Thomas J, Constable A, Wotherspoon S, Raymond B (2013) Testing paradigms of ecosystem change under climate warming in antarctica. PloS ONE 8:e55093.

Melbourne-Thomas J, Wotherspoon S, Raymond B, Constable A (2012) Comprehensive evaluation of model uncertainty in qualitative network analyses. Ecological Monographs 82:505–519.

Metcalf S, Dambacher J, Hobday A, Lyle J (2008) Importance of trophic information, simplification and aggregation error in ecosystem models. Marine Ecology Progress Series 360:25–36.

Metcalf SJ (2010) Qualitative models to complement quantitative ecosystem models for the analysis of data-limited marine ecosystems and fisheries. Reviews in Fisheries Science 18:248–265.

Milborrow S (Accessed October 2014) Multivariate Adaptive Regression Splines, R package version 4.0.0. *http://CRAN.R-project.org/package=earth*

National Research Countil (2010) Ecosystem Concepts for Sustainable Bivalve Mariculture. National Academies Press, Washington D.C., 190 p.

Oksanen J, Blanchet FG, Kindt R, et al. (2013) vegan: Community Ecology Package, R package version 2.0-10. *http://CRAN.R-project.org/package=vegan*

Ortiz M, Wolff M (2002) Application of loop analysis to benthic systems in northern Chile for the elaboration of sustainable management strategies. Marine Ecology Progress Series 242:15–27.

Palacios SL, Zimmerman RC (2007) Response of eelgrass *Zostera marina* to CO_2 enrichment: possible impacts of climate change and potential for remediation of coastal habitats. Marine Ecology Progress Series 344:1–13.

Plaganyi EE, Butterworth DS (2004) A critical look at the potential of ecopath with ECOSIM to assist in practical fisheries management. African Journal of Marine Science 26:261–287.

Puccia CJ, Levins R (1985) Qualitative Modeling of Complex Systems. Harvard University Press Cambridge, 259 p.

R Development Core Team (2014) R: a language and environment for statistical computing, version 3.0.3. R Foundation for Statistical Computing, Vienna.

Raymond B, McInnes J, Dambacher JM, Way S, Bergstrom DM (2011) Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. Journal of Applied Ecology 48:181–191.

Roberts M, Mohamedali T, Sackmann B, Khangaonkar T, Long W (2014) Puget Sound and the Straits Dissolved Oxygen Assessment: impacts of current and future human nitrogen sources and climate change through 2070. Washington Department of Ecology, Olympia, WA, 151 p.

Ruesink JL, Rowell K (2012) Seasonal effects of clams (*Panopea generosa*) on eelgrass (*Zostera marina*) density but not recovery dynamics at an intertidal site. Aquatic Conservation: Marine and Freshwater Ecosystems 22:712–720.

Ruesink JL, Yang S, Trimble AC (2015) Variability in carbon availability and eelgrass (*Zostera marina*) biometrics along an estuarine gradient in Willapa Bay, WA, USA. Estuaries and Coasts 38(6):1908-1917.

Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisehart LM (2006) Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. Marine Ecology Progress Series 311:203–215.

Sanford E, Gaylord B, Hettinger A, Lenz EA, Meyer K, Hill TM (2014) Ocean acidification increases the vulnerability of native oysters to predation by invasive snails. Proceedings of the Royal Society B: Biological Sciences 281:20132681.

Simenstad CA, Fresh KL (1995) Influence of intertidal aquaculture on benthic communities in Pacific Northwest estuaries: scales of disturbance. Estuaries 18:43–70.

Soto D, Aguilar-Manjarrez J, Bermúdez J et al. (2008) Applying an ecosystem-based approach to aquaculture: principles, scales and some management measures. In Soto D, Aguilar-Manjarrez J, Hishamunda N (eds), Building an Ecosystem Approach to Aquaculture, Vol. 14. Proceedings of the Expert Workshop, 7–11 May 2007, Palma de Mallorca, Spain. FAO Fisheries and Aquaculture, Rome, pp. 15–34 plus appendix.

Stohlgren TJ, Ma P, Kumar S, et al. (2010) Ensemble habitat mapping of invasive plant species. Risk Analysis 30:224–235.

Stone L, Roberts A (1991) Conditions for a species to gain advantage from the presence of competitors. Ecology 72:1964–1972.

Tallis HM, Ruesink JL, Dumbauld B, Hacker S, Wisehart LM (2009) Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research 28:251–261.

Thom RM (1996) CO_2-Enrichment effects on eelgrass (*Zostera marina L.*) and bull kelp (*Nereocystis luetkeana* (mert.) P & R.). Water, Air, and Soil Pollution 88(3):383–391.

Timmins-Schiffman E, O'Donnell MJ, Friedman CS, Roberts SB (2012) Elevated pCO_2 causes developmental delay in early larval Pacific oysters, *Crassostrea gigas*. Marine Biology 160:1973–1982.

Toba DR, Thompson DS, Chew KK, Anderson GJ, Miller MB (1992) Guide to Manila clam culture in Washington. Washington Sea Grant, Seattle, Washington, 80 p.

Wagner E, Dumbauld BR, Hacker SD, Trimble AC, Wisehart LM, Ruesink JL (2012) Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina*. Marine Ecology Progress Series 468:149–160.

Waldbusser GG, Brunner EL, Haley BA, Hales B, Langdon CJ, Prahl FG (2013) A developmental and energetic basis linking larval oyster shell formation to acidification sensitivity. Geophysical Research Letters 40:2171–2176.

Whitlatch RB, Osman RW (1994) A qualitative approach to managing shellfish populations: assessing the relative importance of trophic relationships between species. Journal of Shellfish Research 13:229–242

Yodzis P (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology 67:635–658.

Zimmerman RC, Kohrs DG, Steller DL, Alberte RS (1997) Impacts of CO_2 enrichment on productivity and light requirements of eelgrass. Plant Physiology 115:599–607.

APPENDIX

Linkages in Aquaculture–Environment Interactions in South Puget Sound and Willapa Bay

Appendix Table 1. Description of linkages in the South Puget Sound model of aquaculture–environment interactions and primary references where available. Linkage types denoted by an asterisk indicate uncertain interactions (represented as dashed lines in Figure 2). For brevity, only the predator linkage is listed when the predator effect and prey effect in a predator–prey relationship are either both certain or uncertain.

Effect of	Effect on	Type	Comments and references
Scoters	Manila clam	Predator–prey (predator)	Scoters prey on manila clams, reducing clam densities (DeFrancesco and Murray 2010, Lewis et al. 2007).
Manila clam	Scoters	Predator–prey (prey)*	Unclear to what extent scoter populations are driven by Manila clam aquaculture (Žydelis et al. 2006).
Small fishes	Manila clam	Predator–prey*	Unclear if clam loss due to siphon nipping from flatfish and sculpin occurs; unknown if cultured manila clams are important to small fish populations (e.g., Armstrong et al. 1995, Meyer and Byers 2005, Peterson and Quammen 1982).
Small fishes	Structure invertebrates	Predator–prey	Benthic invertebrates are important prey for English sole (Buechner et al. 1981), sculpin (Armstrong et al. 1995, Dinnel et al. 1990, Williams 1994), shiner perch (Troiano et al. 2013).
Small fishes	Non-structure invertebrates	Predator–prey	Benthic invertebrates are important prey for English sole (Buechner et al. 1981), sculpin (Armstrong et al. 1995, Dinnel et al. 1990, Williams 1994), shiner perch (Troiano et al. 2013).
Graceful crab	Manila clam	Predator–prey (predator)	Manila clam loss due to predation by graceful crab (DeFrancesco and Murray 2010).
Graceful crab	Structure invertebrates	Predator–prey	Graceful crab are likely generalist predators, similar to red rock crab (Knudsen 1964). Common in areas with and without aquaculture structure (Brown and Thuesen 2011, McDonald et al. 2015).
Graceful crab	Non-structure invertebrates	Predator–prey	Graceful crab are likely generalist predators, similar to red rock crab (Knudsen 1964). Common in areas with and without aquaculture structure (Brown and Thuesen 2011, McDonald et al. 2015).
Red rock crab	Structure invertebrates	Predator–prey	Generalist predator, may occur in mud habitats (Knudsen 1964, Robles et al. 1989).
Red rock crab	Pacific oyster	Predator–prey	Red rock crab prey on Pacific oyster (Grason and Miner 2012) and prefer oyster bed habitat (Holsman et al. 2006).
Red rock crab	Moon snail/sea stars	Predator–prey	Moon snail and sea stars are preyed upon by red rock crab (PS McDonald, Univ. Washington School of Aquatic and Fisheries Sciences, Seattle, personal communication).
Red rock crab	Manila clam	Predator–prey	Red rock crab prey on cultured Manila clams (Anderson et al. 1982, Boulding and Hay 1984, Chew 1989, Toba et al. 1992).
Chinook salmon	Structure invertebrates	Predator–prey	Predator to benthic invertebrates (Buechner et al. 1981).
Chinook salmon	Zooplankton	Predator–prey	Zooplankton common in Chinook salmon diet (e.g., Duffy et al. 2010, Troiano et al. 2013).
Moon snail/sea stars	Manila clam	Predator–prey*	Known predator of clams (Kozloff 1983, Toba et al. 1992), but unclear if moon snail significantly reduces commercial Manila clam productivity (Cook and Bendell-Young 2010).
Moon snail/sea stars	Structure Invertebrates	Predator–prey	Generalist predators of small sedentary invertebrates (Kozloff 1983).
Moon snail/sea stars	Nonstructure invertebrates	Predator–prey	Moon snail and sea stars both feed on bivalves and other infaunal invertebrates (Kozloff 1983).
Moon snail/sea stars	Pacific oyster	Predator–prey	Known predator of Pacific oyster (DeFrancesco and Murray 2010).
Moon snail/sea stars	Geoduck	Predator–prey (predator)	Sea stars prey on geoduck (Mauzey et al. 1968, Sloan and Robinson 1983, Van Veldhuizen and Phillips 1978), though moon snail predation has not been directly observed (Straus et al. 2013).
Geoduck	Moon snail/sea stars	Predator–prey (prey)*	Unclear if cultured geoduck are important to moon snail/sea star productivity.

Appendix Table 1 · continued

Pacific oyster	Structure invertebrates	Positive	Pacific oyster addition increases epibenthic invertebrate abundance (Dumbauld et al. 2001).
Pacific oyster	Phytoplankton	Negative	Pacific oysters are filter feeders (Wheat and Ruesink 2013).
Zostera marina	Structure invertebrates	Positive	Increase in plant density likely to increase benthic invertebrate abundance (e.g., Attrill et al. 2000).
Z. marina	Chinook salmon	Positive*	*Z. marina* serves as a refuge for Chinook salmon (Semmens 2008), but Chinook salmon are also found in other habitats and associations with *Z. marina* do not appear to be tied to foraging (Dumbauld et al. 2015, Hosack et al. 2006).
Z. marina	Small fish	Positive*	Increase in eelgrass may potentially increase small fish abundance (e.g., Kelly et al. 2008), but is uncertain.
Geoduck	Structure invertebrates	Positive	Increased invertebrate abundance with geoduck farm structures (McDonald et al. 2015).
Geoduck	Phytoplankton	Negative	Geoduck filter feed, consume phytoplankton (Goodwin and Pease 1989).
Structure invertebrates	Phytoplankton	Predator–prey	Structure invertebrates include deposit and filter feeders.
Non-structure invertebrates	Phytoplankton	Predator–prey	Non-structure invertebrates include deposit and filter feeders.
Zooplankton	Phytoplankton	Predator–prey	Zooplankton include filter feeders (Harvey et al. 2012).
Phytoplankton	*Z. marina*	Predator–prey	*Z. marina* likely light-limited at lower end of its distribution (Britton-Simmons et al. 2010, Thom and Albright 1990, Thom et al. 2008).

Appendix Table 2. Details of the interactions within Willapa Bay as depicted in Figure 3. Interactions denoted by asterisks under Type indicate those that are poorly understood (represented by dashed lines in Figure 2). For brevity only the predator linkage is listed when the predator effect and prey effect in a predator–prey relationship are either both certain or uncertain. If certainty differs, predator and prey linkages are noted separately.

Effect of	Effect on	Type	Comments and references
Crows/Gulls	Manila clam	Predator–prey (predator)	Important predators of manila clams in Willapa Bay (DeFrancesco and Murray 2010).
Manila clam	Crows/Gulls	Predator–prey (prey)*	Unknown if manila clam are important to crow/gull population productivity.
Small fishes	Manila clam	Predator–prey*	Potential manila clam loss due to siphon nipping (e.g., by flatfish and sculpin) (Armstrong et al. 1995, Meyer and Byers 2005, Peterson and Quammen 1982, Williams 1994); unknown if important mortality source to Willapa Bay clams.
Small fishes	Non-structure invertebrates	Predator–prey	Benthic invertebrates are important prey for English sole (Buechner et al. 1981), sculpin (Armstrong et al. 1995, Dinnel et al. 1990, Williams 1994), and shiner perch (Troiano et al. 2013).
Small fishes	Structure invertebrates	Predator–prey	Benthic invertebrates are important prey for English sole (Buechner et al. 1981), sculpin (Armstrong et al. 1995, Dinnel et al. 1990, Williams 1994), and shiner perch (Troiano et al. 2013).
Small fishes	Young of year (YOY) Dungeness crab	Predator–prey	Common diet item in sculpin (Armstrong et al. 1995).
Adult Dungeness crab	Manila clam	Predator–prey (predator)	Known predator of Manila clams (e.g., Smith 1996).
Manila clam	Adult Dungeness crab	Predator–prey (prey)*	Unknown if Dungeness crab abundance depends on Manila clams.
Adult Dungeness crab	Non-structure invertebrates	Predator–prey	Dungeness prey on bivalves, small crustaceans (Stevens et al. 1982); prefer mud habitat over oyster and eelgrass (Holsman et al. 2006).
YOY Dungeness crab	Adult Dungeness crab	Positive	YOY Dungeness crab prefer structured habitats over mud (Armstrong et al. 1995 Dumbauld et al. 1993, Eggleston and Armstrong 1994, McMillan et al. 1995) and recruit into the adult population.
Red rock crab	Pacific oyster	Predator–prey	Significant predator–prey interaction (Garson and Miner 2012); red rock crab prefer oyster bed habitat (Holsman et al. 2006).
Red rock crab	Drills	Predator–prey	Significant predator–prey interaction (Garson and Minter 2012).
Red rock crab	Structure invertebrates	Predator–prey	Potential invertebrate prey (Knudsen 1964, Robles et al. 1989); red rock crab prefer structured habitats (Holsman et al. 2006).
Red rock crab	Manila clam	Predator–prey (predator)	Red rock crab prey on cultured Manila clams (Anderson et al. 1982, Boulding and Hay 1984, Chew 1989, Toba et al. 1992).
Manila clam	Red rock crab	Predator–prey (prey)*	Unknown if red rock abundance depends on Manila clams.
Chinook salmon	Zooplankton	Predator–prey	Zooplankton are prey to Chinook salmon in Willapa Bay (Troiano et al. 2013).
Chinook salmon	Structure invertebrates	Predator–prey	Chinook salmon prey on benthic invertebrates (Buechner et al. 1981) that occur in structured habitats (oyster beds, eelgrass; Hosack et al. 2006).
Green sturgeon	Ghost shrimp	Predator–prey (predator)	Predator exclusion experiments indicate green sturgeon can locally impact shrimp densities (Dumbauld et al. 2008).
Ghost shrimp	Green sturgeon	Predator–prey (prey)*	Unknown if ghost shrimp influence green sturgeon abundance.
Z. japonica	Manila Clam	Negative	*Z. japonica* reduces early survival (Ruesink et al. 2014) and growth in Manila clam (Patten 2014, Tsai et al. 2010).
Manila clam	Phytoplankton	Negative	Manila clam are filter feeders.
Z. japonica	Structure invertebrates	Positive	Increased plant density likely increases invertebrate abundance (e.g., Attrill et al. 2000).
Structure invertebrates	Phytoplankton	Predator–prey	Filter feeding invertebrates common in structured habitats (Ferraro and Cole 2007, Hosack et al. 2006).
Pacific oyster	*Z. marina*	Negative	Competition for space (Tallis et al. 2009, Wagner et al. 2012).
Pacific oyster	Structure invertebrates	Positive	Oysters increases epibenthic invertebrate abundance (Dumbauld et al. 2001).
Pacific oyster	Drills	Predator–prey	Drills prey on Pacific oyster (Buhle and Ruesink 2009).

Appendix Table 2 · continued

Drills	Structure invertebrates	Predator–prey	The drill *Urosalpinx cinerea* preys on barnacles, sedentary invertebrates (Kozloff 1983).
Pacific oyster	YOY Dungeness crab	Positive	Habitat and predator refuge (Armstrong et al. 1995, Dumbauld et al. 1993, Eggleston and Armstrong 1995, Fernandez et al. 1993).
Z. marina	YOY Dungeness crab	Positive	Positive association between eelgrass density and Dungeness crab, especially in spring (e.g., McMillan et al. 1995).
Pacific oyster	Phytoplankton	Predator–prey	Modeling evidence (Banas et al. 2007) and field studies (Wheat and Ruesink 2013) indicate drawdown control of phytoplankton.
YOY Dungeness crab	Structure invertebrates	Predator–prey	YOY Dungeness crab feed on benthic invertebrates (Iribarne et al. 1995).
Ghost shrimp	Pacific oyster	Negative	Ghost shrimp destabilize substrate and smother Pacific oysters with sediments (Dumbauld et al. 2006, Feldman et al. 2000).
Ghost shrimp	Non-structure invertebrates	Negative	Decreases sedentary benthic organisms, filter feeders (Posey 1986).
Z. marina	Structure invertebrates	Positive	Increase in plant density likely increases invertebrate abundances (e.g., Attrill et al. 2000) .
Z. marina	Chinook salmon	Positive*	Chinook salmon may have an affinity for *Z. marina* because of prey availability and predator refuge (Semmens 2008), but trawl survey data show no relationship between Chinook salmon abundance and eelgrass (Hosack et al. 2006).
Ghost shrimp	*Z. marina*	Negative	Ghost shrimp may bury seeds, smother eelgrass seedlings (Dumbauld and Wyllie-Echeverria 2003, Harrison 1987)
Ghost shrimp	*Z. japonica*	Negative	Ghost shrimp may bury seeds, smother eelgrass seedlings (Dumbauld and Wyllie-Echeverria 2003, Harrison 1987)
Z. marina	Ghost shrimp	Negative	Eelgrass roots may inhibit burrowing (Harrison 1987).
Z. japonica	Ghost shrimp	Negative	Eelgrass roots may inhibit burrowing (Harrison 1987).
Z. japonica	Structure invertebrates	Positive	Provides habitat for invertebrates (Posey 1988); increase in plant density may increase invertebrate abundance (e.g., Attrill et al. 2000).
Z. japonica	YOY Dungeness crab	Positive	Positive association between eelgrass density and YOY Dungeness crab, especially in spring (McMillan et al. 1995).
Z. japonica	Brant	Positive	Important prey item (Baldwin and Lovvorn 1994a, b); eelgrass area positivity correlated with Brant abundance (Ganter 2000, Wilson and Atkinson 1995).
Z. marina	Brant	Positive	Important prey item (Baldwin and Lovvorn 1994a, b); eelgrass area positivity correlated with Brant abundance (Ganter 2000; Wilson and Atkinson 1995).
Ghost shrimp	Green sturgeon	Predator–prey (prey)*	Unknown if prey abundance is limiting green sturgeon populations (Dumbauld et al. 2008).
Ghost shrimp	Non-structure invertebrates	Negative	Decreases sedentary benthic organisms, filter feeders (Posey 1986).
Mud shrimp	Phytoplankton	Predator–prey	Feeds on phytoplankton, can potentially reduce standing stock (Griffen et al. 2004).
Mud shrimp	Non-structure invertebrates	Negative	Reduction in sedentary invertebrates (Posey et al. 1991).
Phytoplankton	*Z. marina*	Negative	Lower subtidal distribution may be light limited, but results are ambiguous (Thom et al. 2008).
Phytoplankton	*Z. japonica*	Negative	Lower distribution potentially light limited but unresolved (Britton-Simmons et al. 2010, Kaldy 2006).
Phytoplankton	Zooplankton	Predator–prey	Zooplankton are important grazers (e.g., Calbet and Landry 2004).

APPENDIX LITERATURE CITED

Anderson GJ, Miller MB, Chew KK (1982) A guide to Manila clam aquaculture in Puget Sound. Washington Sea Grant Technical Report, Washington Sea Grant Program, College of Ocean and Fishery Sciences, University of Washington, Seattle, 45 p.

Armstrong JL, Armstrong DA, Mathews SB (1995) Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister*. Fishery Bulletin 93:456–470.

Attrill MJ, Strong JA, Rowden AA (2000) Are macroinvertebrate communities influenced by seagrass structural complexity? Ecography 23:114–121.

Baldwin J, Lovvorn J (1994a) Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. Marine Biology 120:627–638.

Baldwin JR, Lovvorn JR (1994b) Expansion of seagrass habitat by the exotic *Zostera japonica*, and its use by dabbling ducks and brant in Boundary Bay, British Columbia. Marine Ecology Progress Series 103:119–127.

Banas N, Hickey B, Newton J, Ruesink J (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecology Progress Series 341:123–139.

Boulding E, Hay T (1984) Crab response to prey density can result in density-dependent mortality of clams. Canadian Journal of Fisheries and Aquatic Sciences 41:521–525.

Britton-Simmons KH, Wyllie-Echeverria S, Day E, et al. (2010) Distribution and performance of the nonnative seagrass *Zostera japonica* across a tidal height gradient on Shaw Island, Washington. Pacific Science 64(2):187–198.

Brown RA, Thuesen EV (2011) Biodiversity of mobile benthic fauna in geoduck (*Panopea generosa*) aquaculture beds in southern Puget Sound, Washington. Journal of Shellfish Research 30:771–776.

Buechner H, Matheson L, Simenstad CA (1981) Food web relationships of juvenile salmonids and English sole. In Simenstad CA, Eggers DH (eds) Juvenile salmonids and baitfish distribution, abundance, and prey resources in selected areas of Grays Harbor, Washington. FRI-UW-8116, Fisheries Research Institute, University of Washington, Seattle, pp. 146–185.

Buhle ER, Ruesink JL (2009) Impacts of invasive oyster drills on Olympia oyster (*Ostrea lurida* Carpenter 1864) recovery in Willapa Bay, Washington, United States. Journal of Shellfish Research 28:87–96.

Calbet A, Landry MR (2004) Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. Limnology and Oceanography 49:51–57.

Chew KK (1989) Manila clam biology and fishery development in western North America. In Manzi JJ, Castagna M (eds) Clam Mariculture in North America. Elsevier, Amsterdam, pp. 243–261.

Cook N, Bendell-Young L (2010) Determining the ecological role of *Euspira lewisii:* part I: feeding ecology. Journal of Shellfish Research 29:223–232.

DeFrancesco J, Murray K (2010) Pest Management Strategic Plan for bivalves in Oregon and Washington. In Clarke D (ed), Summary of a workshop held on March 11, 2010, Long Beach, Washington. Western Integrated Pest Management Center, United States Department of Agriculture, National Institute of Food and Agriculture, 88 p.

Dinnel P, Armstrong JL, Lauth RR, Larsen K, Armstrong D, Sulkin S (1990) Fish predation on dungeness crab in Padilla Bay, Washington. FRI-UW-9001, Fisheries Research Institute, School of Fisheries, University of Washington, Seattle, 69 p.

Duffy EJ, Beauchamp DA, Sweeting RM, Beamish RJ, Brennan JS (2010) Ontogenetic diet shifts of juvenile chinook salmon in nearshore and offshore habitats of Puget Sound. Transactions of the American Fisheries Society 139:803–823.

Dumbauld B, Hosack GR, Bosley KL (2015) Association of juvenile salmon and estuarine fish with intertidal seagrass and oyster aquaculture habitats in Willapa Bay, Washington. Transactions of the American Fisheries Society 144(6):1091–1110.

Dumbauld BR, Armstrong DA, McDonald TL (1993) Use of oyster shell to enhance intertidal habitat and mitigate loss of Dungeness crab (*Cancer magister*) caused by dredging. Canadian Journal of Fisheries and Aquatic Sciences 50:381–390.

Dumbauld BR, Booth S, Cheney D, Suhrbier A, Beltran H (2006) An integrated pest management program for burrowing shrimp control in oyster aquaculture. Aquaculture 261:976–992.

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. Marine Pollution Bulletin 42:826–844.

Dumbauld BR, Holden DL, Langness OP (2008) Do sturgeon limit burrowing shrimp populations in Pacific Northwest Estuaries? Environmental Biology of Fishes 83:283–296.

Dumbauld BR, Wyllie-Echeverria S (2003) The influence of burrowing thalassinid shrimps on the distribution of intertidal seagrasses in Willapa Bay, Washington, USA. Aquatic Botony 77:27–42.

Eggleston DB, Armstrong DA (1995) Pre-and post-settlement determinants of estuarine Dungeness crab recruitment. Ecological Monographs 65:193–216.

Feldman KL, Armstrong DA, Dumbauld BR, DeWitt TH, Doty DC (2000) Oysters, crabs, and burrowing shrimp: review of an environmental conflict over aquatic resources and pesticide use in Washington State's (USA) coastal estuaries. Estuaries 23:141–176.

Fernandez M, Armstrong D, Iribarne O (1993) First cohort of young-of-the-year Dungeness crab, *Cancer magister*, reduces abundance of subsequent cohorts in intertidal shell habitat. Canadian Journal of Fisheries and Aquatic Sciences 50:2100–2105.

Ferraro SP, Cole FA (2007) Benthic macrofauna–habitat associations in Willapa Bay, Washington, USA. Estuarine, Coastal and Shelf Science 71:491–507.

Ganter B (2000) Seagrass (*Zostera spp.*) as food for brant geese (*Branta bernicla*): an overview. Helgoland Marine Research 54:63–70.

Goodwin CL, Pease B (1989) Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest)—Pacific geoduck clam. U.S. Fish and Wildlife Service Biological Reports 82(11.120), 14 p.

Grason EW, Miner BG (2012) Preference alters consumptive effects of predators: top-down effects of a native crab on a system of native and introduced prey. PLoS ONE 7:e51322. doi: 10.1371/journal.pone.0051322.

Griffen BD, DeWitt TH, Langdon C (2004) Particle removal rates by the mud shrimp *Upogebia pugettensis*, its burrow, and a commensal clam: effects on estuarine phytoplankton abundance. Marine Ecology Progress Series 269:223.

Harrison PG (1987) Natural expansion and experimental manipulation of seagrass (*Zostera* spp.) abundance and the response of infaunal invertebrates. Estuarine, Coastal and Shelf Science 24:799–812.

Holsman KK, McDonald P, Armstrong DA (2006) Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. Marine Ecology Progress Series 308:183–195.

Hosack GR, Dumbauld BR, Ruesink JL, Armstrong DA (2006) Habitat associations of estuarine species: comparisons of intertidal mudflat, seagrass (*Zostera marina*), and oyster (*Crassostrea gigas*) habitats. Estuaries and Coasts 29:1150–1160.

Iribarne O, Armstrong D, Fernández M (1995) Environmental impact of intertidal juvenile Dungeness crab habitat enhancement: effects on bivalves and crab foraging rate. Journal of Experimental Marine Biology and Ecology 192:173–194.

Kaldy J (2006) Production ecology of the non-indigenous seagrass, dwarf eelgrass (*Zostera japonica* Ascher. & Graeb.), in a Pacific Northwest estuary, USA. Hydrobiologia 553:201–217.

Kelly JR, Proctor H, Volpe JP (2008) Intertidal community structure differs significantly between substrates dominated by native eelgrass (*Zostera marina* L.) and adjacent to the introduced oyster *Crassostrea gigas* (Thunberg) in British Columbia, Canada. Hydrobiologia 596:57–66.

Knudsen JW (1964) Observations of the reproductive cycles and ecology of the common *Brachyura* and crablike *Anomura* of Puget Sound, Washington. Pacific Science 18(1):3–33.

Kozloff EN (1983) Seashore Life of the Northern Pacific Coast: an Illustrated Guide to Northern California, Oregon, Washington, and British Columbia. University of Washington Press Seattle, 370 p.

Lewis TL, Esler D, Boyd W (2007) Effects of predation by sea ducks on clam abundance in soft-bottom intertidal habitats. Marine Ecology Progress Series 329:131–144.

Mauzey KP, Birkeland C, Dayton PK (1968) Feeding behavior of asteroids and escape responses of their prey in the Puget Sound region. Ecology 49(4):603–619.

McDonald P, Galloway AW, McPeek KC, VanBlaricom GR (2015) Effects of geoduck (*Panopea generosa* Gould, 1850) aquaculture gear on resident and transient macrofauna communities of Puget Sound, Washington, USA. Journal of Shellfish Research 34:189–202.

McMillan RO, Armstrong DA, Dinnel PA (1995) Comparison of intertidal habitat use and growth rates of two northern Puget Sound cohorts of 0+ age Dungeness crab, *Cancer magister*. Estuaries 18:390–398.

Meyer JJ, Byers JE (2005) As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam. Ecology Letters 8:160–166.

Patten K (2014) The impacts of nonnative Japanese eelgrass (*Zostera japonica*) on commercial shellfish production in Willapa Bay, WA. Agricultural Sciences 5:47185.

Peterson CH, Quammen ML (1982) Siphon nipping: Its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). Journal of Experimental Marine Biology and Ecology 63:249–268.

Posey MH (1986) Changes in a benthic community associated with dense beds of a burrowing deposit feeder, *Callianassa californiensis*. Marine Ecology Progress Series 31:15–22.

Posey MH (1988) Community changes associated with the spread of an introduced seagrass, *Zostera japonica*. Ecology 69(4):974–983.

Posey MH, Dumbauld BR, Armstrong DA (1991) Effects of a burrowing mud shrimp, *Upogebia pugettensis* (Dana), on abundances of macro-infauna. Journal of Experimental Marine Biology and Ecology 148:283–294.

Robles C, Sweetnam D, Dittman D (1989) Diel variation of intertidal foraging by *Cancer productus L.* in British Columbia. Journal of Natural History 23:1041–1049.

Ruesink J, Freshley N, Herrold S, Trimble A, Patten K (2014) Influence of substratum on non-native clam recruitment in Willapa Bay, Washington, USA. Journal of Experimental Marine Biology and Ecology 459:23–30.

Semmens BX (2008) Acoustically derived fine-scale behaviors of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) associated with intertidal benthic habitats in an estuary. Canadian Journal of Fisheries and Aquatic Sciences 65:2053–2062.

Sloan N, Robinson S (1983) Winter feeding by asteroids on a subtidal sandbed in British Columbia. Ophelia 22:125–140.

Smith M (1996) Manila clam aquaculture in shrimp-infested mudflats. MS degree, Oregon State University, Corvallis, OR.

Stevens B, Armstrong D, Cusimano R (1982) Feeding habits of the Dungeness crab *Cancer magister* as determined by the index of relative importance. Marine Biology 72:135–145.

Straus KM, Crosson LM, Vadopalas B (2013) Effects of geoduck aquaculture on the environment: a synthesis of current knowledge. Washington Sea Grant, College of the Environment, University of Washington, Seattle, 47 p.

Tallis HM, Ruesink JL, Dumbauld B, Hacker S, Wisehart LM (2009) Oysters and aquaculture practices affect eelgrass density and productivity in a Pacific Northwest estuary. Journal of Shellfish Research 28:251–261.

Thom R, Albright R (1990) Dynamics of benthic vegetation standing-stock, irradiance, and water properties in central Puget Sound. Marine Biology 104:129–141.

Thom RM, Southard SL, Borde AB, Stoltz P (2008) Light requirements for growth and survival of eelgrass (*Zostera marina* L.) in Pacific Northwest (USA) estuaries. Estuaries and Coasts 31:969–980.

Toba DR, Thompson DS, Chew KK, Anderson GJ, Miller MB (1992) Guide to Manila clam culture in Washington. Washington Sea Grant Program, College of Ocean and Fishery Sciences, University of Washington, Seattle, 80 p.

Troiano AT, King KA, Grue CE, Grassley JM, Ekblad CJ (2013) Brain acetylcholinesterase activity in shiner perch (*Cymatogaster aggregata*) and juvenile chinook salmon (*Oncorhynchus tshawytscha*) after application of carbaryl to control burrowing shrimp within Willapa Bay, Washington. Archives of Environmental Contamination and Toxicology 65:779–789.

Tsai C, Yang S, Trimble AC, Ruesink JL (2010) Interactions between two introduced species: *Zostera japonica* (dwarf eelgrass) facilitates itself and reduces condition of *Ruditapes philippinarum* (Manila clam) on intertidal flats. Marine Biology 157:1929–1936.

Van Veldhuizen H, Phillips D (1978) Prey capture by *Pisaster brevispinus* (Asteroidea: Echinodermata) on soft substrate. Marine Biology 48:89–97.

Wagner E, Dumbauld BR, Hacker SD, Trimble AC, Wisehart LM, Ruesink JL (2012) Density-dependent effects of an introduced oyster, *Crassostrea gigas*, on a native intertidal seagrass, *Zostera marina* 468:149–160.

Wheat E, Ruesink JL (2013) Commercially-cultured oysters (*Crassostrea gigas*) exert top-down control on intertidal pelagic resources in Willapa Bay, Washington, USA. Journal of Sea Research 81:33–39.

Williams GD (1994) Effects of a large-scale estuarine intertidal habitat modification on distribution patterns and food habits of epibenthic fish species in Grays Harbor, Washington. MS degree, School of Fisheries, College of Ocean and Fishery Sciences, University of Washington Seattle.

Wilson UW, Atkinson JB (1995) Black brant winter and spring-staging use at two Washington coastal areas in relation to eelgrass abundance. Condor 97:91–98.

Žydelis R, Esler D, Boyd WS, Lacroix DL, Kirk M (2006) Habitat use by wintering surf and white-winged scoters: effects of environmental attributes and shellfish aquaculture. Journal of Wildlife Management 70:1754–1762.

An Oceanographic Circulation Model for South Puget Sound

Neil S Banas, University of Washington (UW) School of Oceanography; Wei Cheng, UW Joint Institute for the Study of the Atmosphere and Ocean

ABSTRACT

A new, high-resolution (200 meter) circulation model for South Puget Sound was developed, both to illuminate water connectivity and residence-time patterns with application to South Puget Sound shellfish aquaculture and, as a pilot effort, to construct efficient methods for nesting high-resolution submodels within the model framework run by the University of Washington Coastal Modeling Group. A six-week simulation of late summer, low riverflow conditions (1 August to 15 October 2006) was performed, nested within a previously published full-year simulation of Puget Sound and the adjacent coastal ocean. Comparisons with tide-gauge records from Seattle and Tacoma show that the South Puget Sound model inherits the tidal-height performance of the larger model with almost no further modification. Modeled surface and bottom temperatures in the South Puget Sound domain show good agreement with Washington Department of Ecology monitoring data at 10 stations, although salinity stratification is likely biased by the omission of small, local freshwater sources in the model.

In the model, virtual particles (148,320 total) were released at the surface in each grid cell within South Puget Sound every six hours for the first 14 days of the model run and tracked in three dimensions. In general, the surface particles dispersed across South Puget Sound in a few days, with a mean motion toward the deep central channels and Main Basin from each of the fringing inlets. Results also suggest a strong gradient in residence time from the central, deep channels to the small, western inlets, creating a potential for localized effects on water quality that a bulk analysis would not resolve. A map of "drawdown time" — the time required for cultured shellfish to reduce the standing stock of phytoplankton by 50%, given their inlet-scale densities — was estimated and compared with the map of residence time. Results suggest that Henderson Inlet, Eld Inlet, Totten Inlet, Hammersley Inlet, Oakland Bay, and upper Case Inlet have combinations of long residence time and high densities of aquacultured filter-feeders such that aquaculture operations there may potentially control local phytoplankton concentrations. This is strong motivation to further investigate both the possible downstream effects on other consumers of phytoplankton and the possible role of aquaculture in mitigating eutrophication in western South Puget Sound.

INTRODUCTION

Recent advances have occurred in an effort to build a multi-scale biological–chemical–physical model of Puget Sound and its adjacent coastal waters that can link both local and large-scale stressors (e.g., land-use pressure, climate change, ocean acidification) to their impact on habitat for wild and cultured aquatic species. A high level of spatial detail is required if such a model is to inform management, policy, and site-specific concerns. This phase of work has focused on spatial resolution and developing tools to smoothly nest high-resolution submodels within the regional models run by the UW Coastal Modeling Group (CMG), using South Puget Sound as a test case.* The South Puget Sound work has been coordinated with a parallel effort through the Washington Ocean Acidification Center to add short-term forecasting ability and carbon chemistry to the CMG Cascadia model (Davis et al. 2014, Giddings et al. 2014, Siedlecki et al. 2015). Together, these efforts point the way toward an operational oxygen/pH early-warning system for Puget Sound and its surrounding waters.

This class of oceanographic model has many other potential applications; for example, analysis of pollution and sewage dispersal, larval supply and population connectivity, and the issue that has been focused on in this pilot effort: coupling between benthic grazers (such as cultured shellfish) and their phytoplankton diet. In general, benthic filter feeders in shallow estuaries limit and are limited by phytoplankton in the water column. The balance among local phytoplankton production, hydrodynamic import and export, shellfish consumption rates, and consumption and recycling by other grazers like zooplankton controls the carrying capacity of the system for shellfish production. In systems near their carrying capacity, food competition can arise both among filter feeders and between them and other biota. For example, previous work (Banas et al. 2007) sponsored by Washington Sea Grant demonstrated that in Willapa Bay, cultured shellfish and other benthic grazers appear to control phytoplankton concentrations. Consequently, aquaculture in Willapa Bay may be nearing a point of diminishing returns, where adding one more oyster increases total oyster productivity but decreases the average oyster's food intake. In systems where the leading concern is not undersupply but rather oversupply of phytoplankton (i.e., systems vulnerable to eutrophication†, such as some South Puget Sound inlets), the same calculation of phytoplankton drawdown in relation to supply indicates the potential for aquaculture to mitigate water quality concerns. This section describes the South Puget Sound model setup; comparisons with tide-gauge, temperature, and salinity data; an analysis of residence time and connectivity in South Puget Sound in late summer; and finally, an exploratory analysis of phytoplankton drawdown potential.

---

* *http://faculty.washington.edu/pmacc/cmg/cmg.html*

† Overgrowth of phytoplankton, often associated with water quality problems such as low oxygen.

MATERIALS AND METHODS

The Model

The South Puget Sound model was implemented in ROMS (Regional Ocean Modeling System; Haidvogel et al. 2000), an oceanographic community standard for hydrodynamic and biophysical modeling. The South Puget Sound model is one-way nested within the Puget Sound and adjacent coast model of Sutherland et al. (2011) — the "Salish" model — which is in turn nested within the global Navy Coastal Ocean Model (Barron et al. 2006, 2007). The Salish model has variable horizontal resolution, generally 300–1,000 meters across Puget Sound and the southern Salish Sea; the nested South Puget Sound model has a constant resolution of 200 meters as far north as Tacoma Narrows, expanding to 800 meters in a transition region in southern Main Basin. The model has 30 vertical levels, which use terrain-following coordinates. Output is saved hourly.

This pilot study conducted a six-week simulation of late summer, low riverflow conditions, August 1–October 15, 2006, driven by the full year 2006 simulation described by Sutherland et al. (2011). Tidal and water-property signals were passed from the Salish model to the South Puget Sound model through an open boundary near Seattle (Figure 1). The South Puget Sound model additionally received direct input from the Duwamish, Puyallup, Nisqually, and Deschutes rivers (Banas et al. 2014, Sutherland et al. 2011), and heat fluxes and wind stress from the the MM5 atmospheric model (Mass et al. 2003), following the methods described by Sutherland et al. (2011). The South Puget Sound model includes wetting and drying of the intertidal zone, unlike the Salish model, which has a minimum water depth of 4 meters. Bathymetry is interpolated from the Finlayson (2005) digital elevation model.

RESULTS AND DISCUSSION

Comparison with Observations

Modeled and observed tidal heights at Seattle and Tacoma were compared (Table 1) for both the Salish model and the South Puget Sound model nested within it. As described by Sutherland et al. (2011), the amplitudes of the semi-diurnal tides (the M2, S2 constituents) are biased low by approximately 25%, an error which likely resulted from under-resolved topographic mixing or a bias in the resonance characteristics (i.e., interaction between incoming and reflected, outgoing waves, or amphidromic structure) of the modeled Puget Sound/Strait of Georgia system as a whole. For purposes of this study, the significant result is that the South Puget Sound model inherits the tidal-height performance of the Salish model with almost no further modification.

Comparisons between the South Puget Sound model and in situ surface and bottom temperature and salinity were performed at Washington Department of Ecology stations that were regularly occupied ($n \geq 9$) in 2006 (Figure 2; see Sutherland et al. 2011 for a much more extensive comparison between the Salish model and hydrographic data). Within the six-week study period, there were 17 observations across these stations. Modeled surface and bottom temperatures ($n = 34$) show good agreement with these observations ($r^2 = 0.56$, mean bias 0.24°C, ratio of standard deviation 1.07). This is indirect evidence that the balance of local heating (which is presumably accentuated in both model and reality by the extensive shallows in the region) and flushing toward deeper water is approximately correct in the model. Modeled salinities ($n = 33$, omitting one bad value) are significantly correlated with the observations (r^2

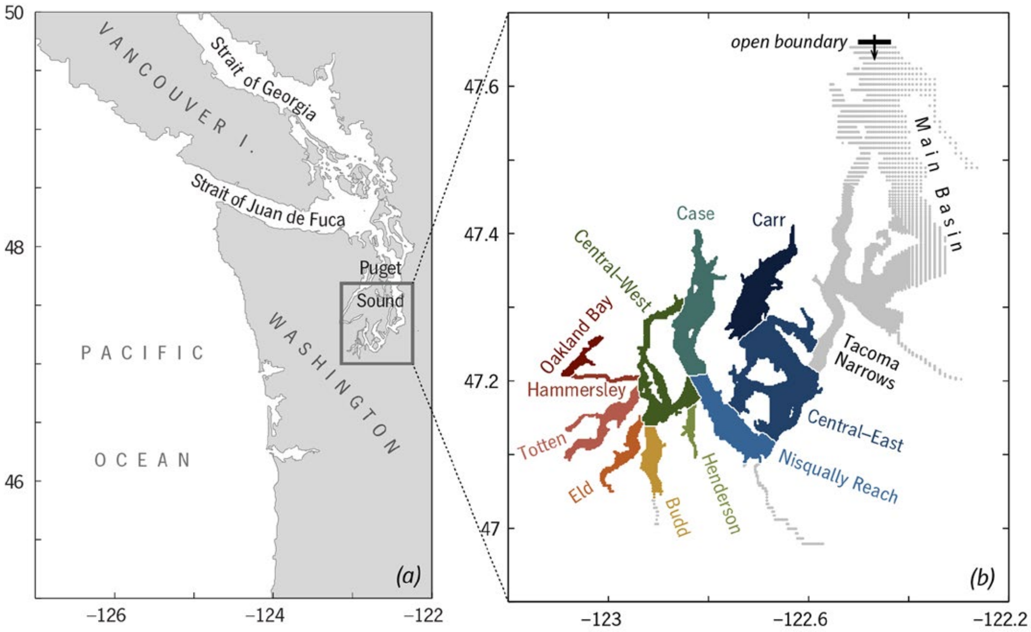


Figure 1. (A) Extent of the Sutherland et al. (2011) "Salish" model domain. (B) South Puget Sound model domain, showing the open boundary where signals from the Salish model are passed in and definitions of the inlets used in the connectivity analysis.

Table 1. Comparison between modeled and observed phase and amplitude of the three leading tidal constituents for the Sutherland et al. (2011) Salish model, and the new South Puget Sound model nested within it. Results are reported for tide gauges at Seattle and Tacoma. An amplitude ratio of 1 and phase difference of 0 would indicate perfect performance.

	M2		**S2**		**K1**	
	Amplitude ratio	**Phase difference**	**Amplitude ratio**	**Phase difference**	**Amplitude ratio**	**Phase difference**
Salish model						
Seattle	0.76	11.8	0.76	10.2	1.02	-3.6
Tacoma	0.76	11.5	0.77	9.5	1.02	-3.5
South Puget Sound model						
Seattle	0.75	22.6	0.77	24.1	1.03	1.2
Tacoma	0.73	24.2	0.76	24.5	1.02	2.4

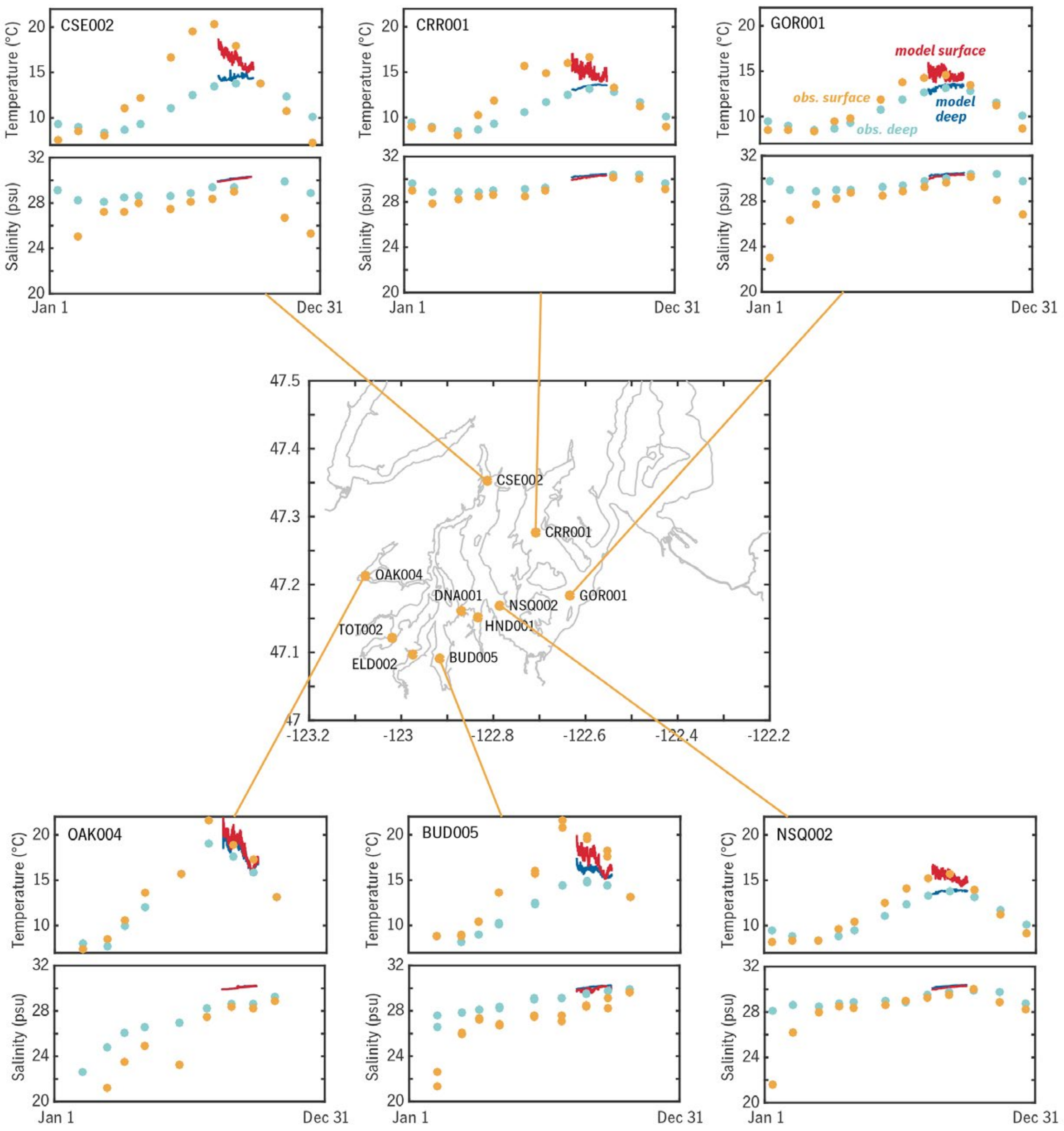


Figure 2. Annual cycles of surface and bottom salinity and temperature at six Washington Department of Ecology monitoring stations in South Puget Sound, Jan–Dec 2006. The locations of these and four other stations included in the statistical model validation described in the text are shown in the central panel. Approximately monthly in situ observations are shown in orange (surface) and light blue (bottom); hourly time series from the six-week South Puget Sound model run is shown in red (surface) and dark blue (bottom).

= 0.51) but biased somewhat high (mean bias 0.9 psu (practical salinity units)) and with reduced variance (ratio of standard deviations 0.24). The bias is comparable with that reported by Sutherland et al. (2011) for the Salish model, and thus is probably inherited directly from that model. Although not the only cause, one cause of the reduced variance is under-stratification in the South Puget Sound model (Figure 2; note that this phenomenon is on a different time and space scale from the more general stratification validation presented by Sutherland et al. 2011). Since tidal amplitude and thus tidal mixing is biased low, not high, the lack of local salinity stratification may reflect the omission of small freshwater inputs other than the four major rivers mentioned previously.

Estimating the effect of bias in stratification and tidal amplitude on overall residence time is not straightforward. To the extent that South Puget Sound is flushed by baroclinic, river-driven mechanisms, both the low stratification and low tidal amplitude suggest an upward bias in estimated flushing rate. In terms of flushing due to tidal dispersion, the low tidal amplitude suggests a downward bias. To the extent that it is flushed by wind-driven circulation, both of these measures may be irrelevant to flushing rate. Progress on this front — better diagnosis of model biases, and resolution of them — will require analysis of a full seasonal cycle and detailed comparisons with process studies such as Edwards et al. (2007).

Residence Time and Connectivity

As in other Pacific Northwest estuaries (Hickey and Banas 2003), late summer is the low riverflow season in Puget Sound, during which river-driven estuarine circulation is expected to be at a minimum and residence time, particularly for surface waters, to be longer than at other times of year. Note that wind-driven circulation may complicate this picture in some inlets (Edwards et al. 2007), as an analysis across a full annual cycle could elucidate in future work.

Virtual particles were released in the model at the surface in each grid cell within South Puget Sound (colored areas, Figure 1) every six hours for the first 14 days of the model run to uniformly sample a full spring–neap cycle (2,643 release locations, 148,320 particles total). Particles were tracked in three dimensions, taking vertical mixing into account, following the methods described in Banas et al. (2014). In general, particles dispersed across South Puget Sound in a few days (illustrated for a few representative inlets, Figure 3). The mean motion of surface particles is seaward, toward the deep central channels and Main Basin, from each of the fringing inlets. This is consistent with the typical structure of tidally averaged estuarine circulation (inflow at depth, outflow at the surface), although the particle-tracking experiment described here may obscure more complex transient or localized patterns, such as wind-driven reversals or flow structures with more than two layers.

This detailed particle experiment allows mapping which subregions of South Puget Sound are "downstream" of others, and includes time lags between them (Figure 4; see Banas et al. 2014 for a comparable analysis on a larger spatial scale). In general, eastern South Puget Sound is downstream of western South Puget Sound, with the "Central–West" inlet (Figure 1) forming a natural dividing line. Note that much of the overall volume–flux pattern simply reflects the relative volumes or surface areas of the "from" and "to" inlets. Although most of the flux from Case Inlet is found in eastern South Puget Sound (or beyond, in Main Basin) after approximately one week, because of its relative size, a measurable fraction of Case Inlet water is found in the small western inlets (Budd, Eld, Totten, Hammersley/Oakland Bay) also after about one week. Budd, Eld, and Totten inlets exchange non-negligible amounts of surface water on the same timescale.

The time required for the median particle to exit the source basin is one convenient measure of the residence time. Note that this metric is scale-dependent, and so residence times for each inlet individually are different from the residence time of particles from each inlet in South Puget Sound as a whole (Figure 5, Table 2). Since this analysis resolves the exit pathways of surface water only, the overall residence time of South Puget Sound as a whole (14 days) is somewhat lower than that calculated by Sutherland et al. (2011) for water at all depths. The median surface-water particle in each inlet is found to exit its inlet in less than one week, although the median particle from each of the fringing inlets is still found somewhere in South Puget Sound after two weeks. Water from Oakland Bay dispersed from South Puget Sound too slowly to calculate a median residence time from this six-week model run.

Overall, these results suggest that while tidal flushing of South Puget Sound is quite efficient on average, the gradient in residence time from the central, deep channels to the small, western inlets is quite strong, potentially creating localized effects on water quality that a bulk analysis would not resolve. This pattern is motivation for returning to the initial question that promped this study: Where in South Puget Sound might cultured shellfish significantly affect phytoplankton biomass?

Phytoplankton-Drawdown Potential

In general, the balance of (i) local phytoplankton production, (ii) hydrodynamic import and export, and (iii) filter feeder consumption rates controls the carrying capacity of a shallow estuary for filter-feeder production (Cloern 1982, Dame and Prins 1988, Peterson and Black 1987). The same balance determines the potential for benthic filter feeders to act as a brake on eutrophication. In systems near their carrying capacity, food competition can arise both among filter feeders and between them and other biota. The balance of (i), (ii), and (iii) needs to be considered across a range of scales — from the system down to individual mudflats — and so it is not straightforward to determine a priori whether a given aquaculture region is near its carrying capacity or capable of causing "downstream" effects on other ecosystem components, whether positive or negative, via depletion of phytoplankton.

The full balance of (i), (ii), and (iii) cannot be assessed using the present version of the model, but an upper bound can be placed on the potential for local benthic control of phytoplank-

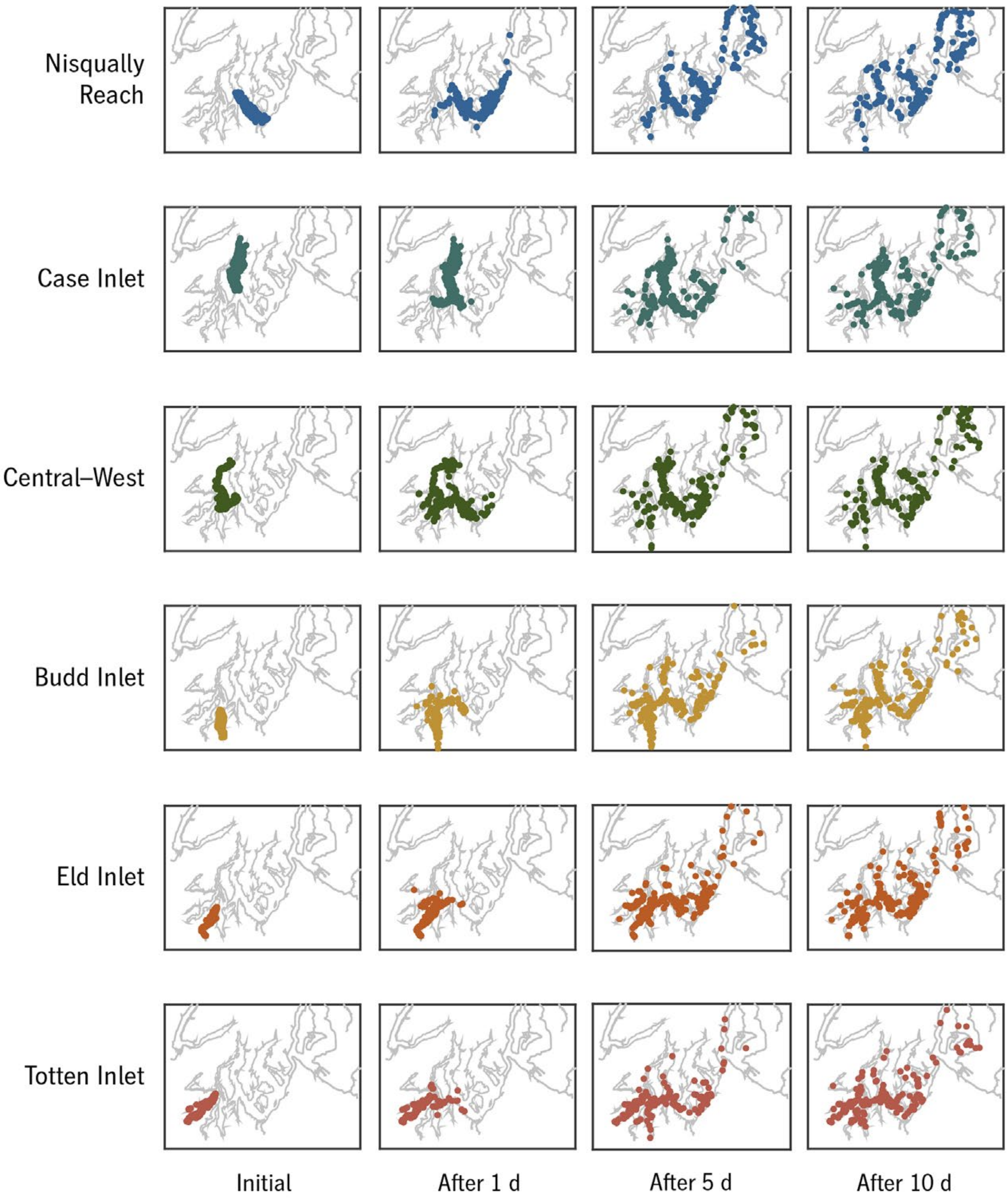
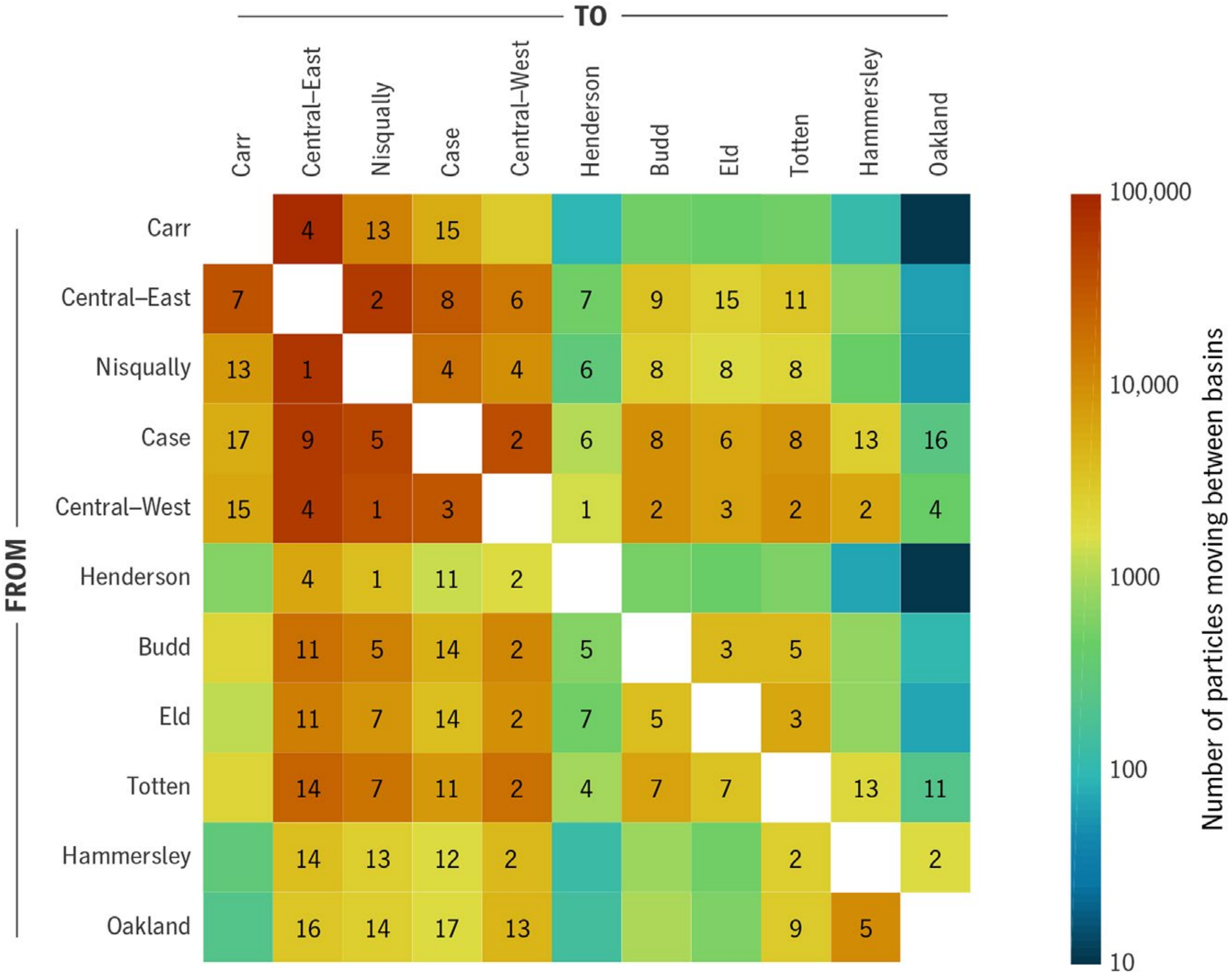


Figure 3. Dispersion of model particles released at the surface in each of six inlets initially and after 1, 5, and 10 days of transport.



	Carr	Central–East	Nisqually	Case	Central–West	Henderson	Budd	Eld	Totten	Hammersley	Oakland
Carr		4	13	15							
Central–East	7		2	8	6	7	9	15	11		
Nisqually	13	1		4	4	6	8	8	8		
Case	17	9	5		2	6	8	6	8	13	16
Central–West	15	4	1	3		1	2	3	2	2	4
Henderson		4	1	11	2						
Budd		11	5	14	2	5		3	5		
Eld		11	7	14	2	7	5		3		
Totten		14	7	11	2	4	7	7		13	11
Hammersley		14	13	12	2				2		2
Oakland		16	14	17	13				9	5	

Figure 4. Connectivity among South Puget Sound inlets. Color indicates the total number of model particles found to move from one inlet to another (note the logarithmic scale). Superimposed numbers indicate the time lag of the peak transport for each connection. Small-volume connections equivalent to <5% of the particles leaving the "from" basin and entering the "to" basin are unlabeled.

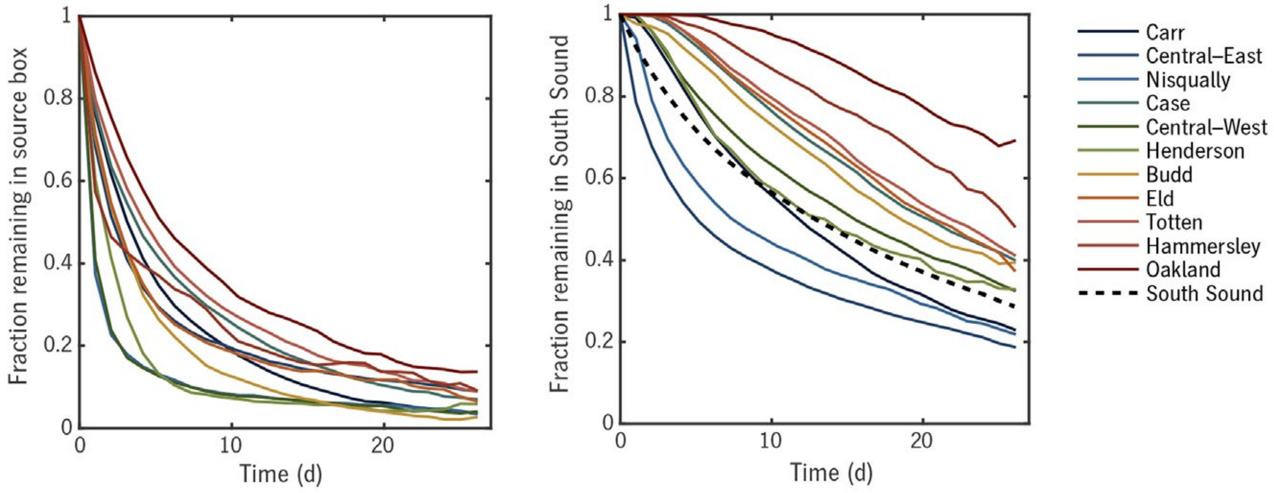


Figure 5. Fraction of model particles remaining in each source basin and in South Puget Sound as a whole over time. Time is measured as days since particles were released; releases occurred at six-hour intervals for 14 days and have been conflated. The time at which each curve crosses 0.5 is the median residence time.

Table 2. Median residence time in the source inlets and in South Puget Sound as a whole for surface water in each inlet shown in Figure 1.

	Median residence time in source inlet (days)	Median residence time in South Puget Sound (days)
Carr Inlet	4	13
Central–East	3	5
Nisqually Reach	1	8
Case Inlet	4	21
Central–West	1	16
Henderson Inlet	2	14
Budd Inlet	3	19
Eld Inlet	3	21
Totten Inlet	5	22
Hammersley Inlet	2	26
Oakland Bay	6	>28
Total	—	14

ton standing stock at each location in the model domain. A benthic clearance rate (in m^3 of overlying water per m of benthic area per s, or m s^{-1}) was estimated for each inlet shown in Figure 1, based on multiplying cultured shellfish density (g$_{\text{dry}}$ km^{-2}) by shellfish clearance rate (L hr^{-1} g$_{\text{dry}}$$^{-1}$) and the proportion of total South Puget Sound cultivated area. Clearance rates were then summed across species to obtain the total water filtered by region (see Appendix for additional details, p. 67). The depletion of an initial phytoplankton concentration P by benthic grazers with clearance rate α follows:

$$\frac{1}{P}\frac{dP}{dt} = \frac{\alpha}{h}$$

where h is water depth (See Banas et al. 2007, Lucas et al. 1999 for a fuller treatment). This describes an exponential decay whose timescale can be written as follows:

$$T_{drawdown} = \frac{ln\ 2}{86400}\ \frac{1}{f_{shallow}}\ \frac{h_{graz}}{\alpha}$$

Here, f_{shallow} denotes the fraction of time a given model particle spends in shallow water overlying benthic grazers, and h_{graz} the typical water-column depth experienced during those conditions (this study assumed two meters). The leading coefficients make T_{drawdown} an estimate of the time, in hours, required for this type of intermittent benthic grazing to reduce an initial phytoplankton population by half. It is thus directly comparable with the median residence time calculated previously, denoted T_{res}. If $T_{drawdown} >> \mathrm{T}_{\text{res}}$, then the circulation is likely to flush phytoplankton from the area too fast for benthic grazers to have much effect, and the likely balance for the phytoplankton budget is between growth and advection. If $\mathrm{T}_{\text{drawdown}} << T_{res}$, then it is possible for benthic grazing to constitute the dominant loss term, and the phytoplankton budget is likely a balance between local growth and local pelagic and benthic grazing.

$T_{drawdown}$ was calculated for each model particle and averaged results were calculated by release location. Maps of $T_{drawdown}$ and T_{res} are shown in Figure 6. To emphasize the (very approximate) threshold where $T_{drawdown}$ and T_{res} balance, values of $T_{drawdown}$ longer than T_{res} are blanked out (gray). As a simple sensitivity test, $T_{drawdown}$ was also calculated using uniform high (10^{-4} m s^{-1}) and low (10^{-5} m s^{-1}) values for α in place of the spatially explicit best guess described previously.

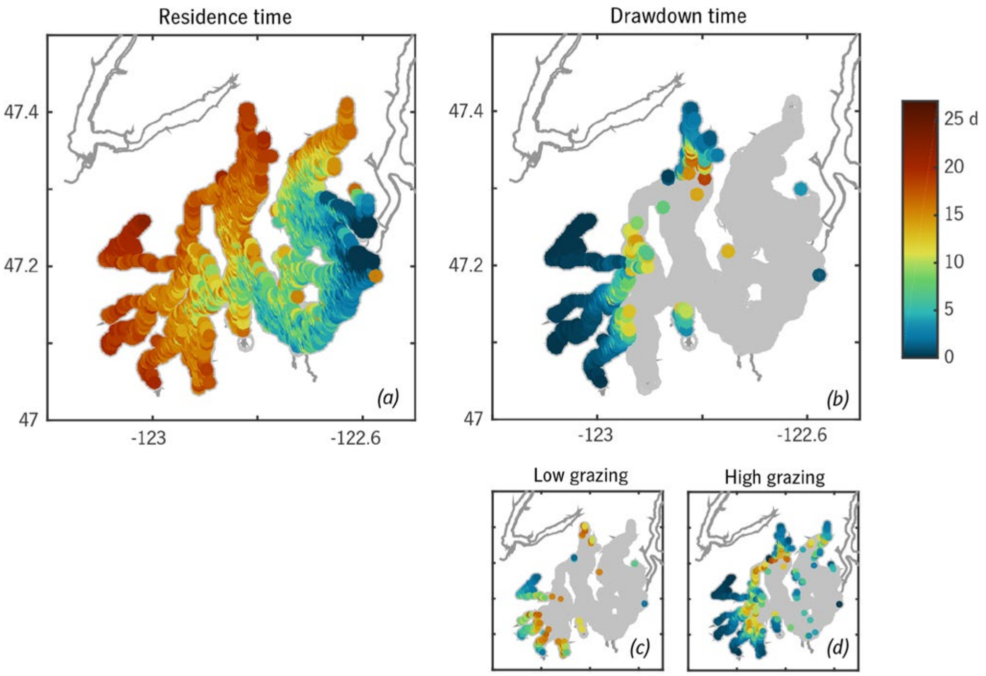


Figure 6. Timescales of (a) flushing by physical processes and (b) depletion of phytoplankton by aquacultured benthic grazers. Areas with drawdown time longer than residence time are shown in gray. (c,d) Comparison cases in which drawdown time was estimated using spatially uniform high and low estimates of benthic clearance rate.

The criterion for potential local control by benthic grazers is met in Henderson, Eld, Totten, Hammersley, and upper Case inlets, and Oakland Bay. This is strong motivation for further study, via both observations and modeling, of coupling between phytoplankton, cultured shellfish, and water quality in these systems.

CONCLUSION

This project served as a pilot study for incorporating high-resolution submodels and intertidal processes into the regional hindcast/forecast model under development by the UW Coastal Modeling Group. The potential for model forecasts on scales relevant to aquaculture operations in South Puget Sound is high. This project also served as a first, approximate mapping of the areas of strong potential interaction between aquaculture and total phytoplankton production. Based on the preceding results, one might hypothesize that the small inlets of western South Puget Sound experience noticeable food competition between cultured bivalves and other consumers of phytoplankton. One might also hypothesize that these inlets are at noticeably lower risk of eutrophication than they would be in the absence of shellfish aquaculture. Methodologically, the results indicate that future modeling of biogeochemistry and water quality in South Puget Sound needs to take the benthic grazer population into account, much as Banas et al. (2007) found was true for Willapa Bay.

ACKNOWLEDGMENTS

Many thanks to Parker MacCready and other members of the UW Coastal Modeling Group for their help with experiment design and troubleshooting. Ryan McCabe performed the tidal-height model intercomparison. Thanks as well to the Washington State Department of Ecology for providing their water quality monitoring data.

LITERATURE CITED

Banas NS, Hickey BM, Newton JA, Ruesink JL (2007) Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecology Progress Series 341:123–139.

Banas NS, Conway-Cranos L, Sutherland DA, MacCready P, Kiffney P, Plummer M (2014) Patterns of river influence and connectivity among subbasins of Puget Sound, with application to bacterial and nutrient loading. Estuaries and Coasts 38:735–753.

Barron CN, Kara AB, Martin PJ, Rhodes RC, Smedstad LF (2006) Formulation, implementation and examination of vertical coordinate choices in the Global Navy Coastal Ocean Model (NCOM). Ocean Modelling 11:347–375.

Barron CN, Smedstad LF, Dastugue JM, Smedstad OM (2007) Evaluation of ocean models using observed and simulated drifter trajectories: Impact of sea surface height on synthetic profiles for data assimilation. Journal of Geophysical Research Oceans 112:C07019. doi:10.1029/2006JC003982.

Cloern JE (1982) Does the benthos control phytoplankton biomass in south San Francisco Bay (USA)? Marine Ecology Progress Series 9:191–202.

Dame RF, Prins TC (1998) Bivalve carrying capacity in coastal ecosystems. Aquatic Ecology 31:409–421.

Davis KA, Banas NS, Giddings SN, Siedlecki SA, MacCready P, Lessard EJ, Kudela RM, Hickey BM (2014) Estuary-enhanced upwelling of marine nutrients fuels coastal productivity in the U.S. Pacific Northwest. Journal of Geophysical Research Oceans 119:8778–8799.

Edwards KA, Kawase M, Sarason CP (2007) Circulation in Carr Inlet, Puget Sound, during spring 2003. Estuaries and Coasts 30:945–958.

Finlayson DP (2005) Combined bathymetry and topography of the Puget Lowland, Washington State. University of Washington School of Oceanography. Available at *www.ocean.washington.edu/data/pugetsound/psdem2005.html*.

Giddings SN, MacCready P, Hickey BM, Banas NS, Davis KA, Siedlecki SA, Trainer VL, Kudela RM, Pelland NA, Connolly TP (2014) Hindcasts of potential harmful algal bloom transport pathways on the Pacific Northwest coast. Journal of Geophysical Research Oceans 119(4):2439–2461.

Haidvogel DB, Arango HG, Hedstrom K, Beckmann A, Rizzoli PM, Shchepetkin AF (2000) Model evaluation experiments in the North Atlantic Basin: Simulations in nonlinear terrain-following coordinates. Dynamics of Atmospheres and Oceans 32:239–281.

Hickey BM, Banas NS (2003) Oceanography of the US Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries and Coasts 26:1010–1031.

Lucas LV, Koseff JR, Cloern JE, Monismith SG, Thompson JK (1999) Processes governing phytoplankton blooms in estuaries. I: The local production-loss balance. Marine Ecology Progress Series 187:1–15.

Mass CF, Albright M, Ovens D, et al. (2003) Regional environmental prediction over the Pacific Northwest. Bulletin of the American Meteorological Society 84:1353–1366.

Peterson CH, Black R (1987) Resource depletion by active suspension feeders in tidal flats—influence of local density and tidal elevation. Limnology and Oceanography 32:143–166.

Siedlecki SA, Banas NS, Davis KA, Giddings S, Hickey BM, MacCready P, Connolly T, Geier S (2015) Seasonal and interannual oxygen variability on the Washington and Oregon continental shelves. Journal of Geophysical Research Oceans 120:608–633.

Sutherland DA, MacCready P, Banas NS, Smedstad LF (2011) A model study of the Salish Sea Estuarine Circulation. Journal of Physical Oceanography 41:1125-43.

Appendix

FILTERING CAPACITY CALCULATIONS

Bridget E Ferris, Washington Sea Grant

An estimate of the filtering capacity of cultured bivalves in South Puget Sound was calculated. Specifically, the study focused on the filtering capacity of the three species that account for the vast majority of harvest in the region: Pacific oyster (*Crassostrea gigas*), Manila clam (*Venerupis philippinarum*), and geoduck (*Panopea generosa*). An overview is provided of the procedure followed by additional detailed information on specific calculations in the following subsections.

Overview

Filtering capacity was estimated by multiplying bivalve density (g_{dry} km^{-2}) and clearance rate estimates (L hr^{-1} $g_{dry}{}^{-1}$) with the proportion of area cultivated in each Washington Department of Fish & Wildlife (WDFW) aquaculture district in South Puget Sound and then normalizing to obtain a species- and district-specific weighted filtering capacity (L hr^{-1} $g_{dry}{}^{-1}$). Filtering capacity was then summed across species to obtain the total water filtered within each WDFW aquaculture district. Filtration rate (L hr^{-1} $g_{dry}{}^{-1}$) was converted to m s^{-1} (the equivalent of m^3 s m^{-2} or volume (m^3) of water filtered per second by a given density (m^2) of bivalves (Banas et al. 2007)) to facilitate calculation of potential phytoplankton drawdown in the South Puget Sound circulation model (Table 1).

Density Calculations

Standing stock density (kg km^{-2}) was calculated based on harvest biomass and age of harvest, following Banas et al. (2007). For each bivalve species, density was estimated following the formula:

$$Density = \frac{1}{Cultivated\ area} \cdot \frac{Annual\ harvest}{Fraction\ of\ standing\ stock\ harvest\ annually}$$

Species-specific, estimates of aquaculture harvest for each WDFW aquaculture district in South Puget Sound in 2010 were obtained from WDFW and summarized by the Pacific Shellfish Institute (Table 2). For each species, published estimates of age of harvest (Table 3) were used, and an equal ratio of plots at each year within the planting/harvesting cycle was assumed. For example, a Manila clam is harvested at age 3, and thus the standing stock would equal $1/3m+2/3m+m$ where m is the density of a mature harvestable bed. In this scenario, harvest equals half the standing stock. Here, linear growth (Banas et al. 2007) and no temporal trend in planting or harvesting were assumed (PS McDonald, Univ. Washington School of Aquatic and Fishery Sciences, T King, Washington Sea Grant, personal communication).

Appendix Table 1. Filtering capacity of cultured Pacific oyster, Manila clam, and geoduck in Washington Department of Fish & Wildlife (WDFW) aquaculture districts in South Puget Sound.

	Filtering capacity			
District	**L h^{-1} km^{-2}**	**L h^{-1} m^{-2}**	**L s^{-1} m^{-2}**	**m3 s^{-1} m^{-2}**
41A	0.00E+00	0.00E+00	0.00E+00	0.00E+00
41B	1.77E+05	1.77E-01	2.95E-03	2.95E-06
41C	7.21E+05	7.21E-01	1.20E-02	1.20E-05
41D	5.03E+06	5.03E+00	8.38E-02	8.38E-05
41E	8.96E+06	8.96E+00	1.49E-01	1.49E-04
41F	2.34E+06	2.34E+00	3.90E-02	3.90E-05
41G	1.24E+07	1.24E+01	2.06E-01	2.06E-04
41H	1.50E+07	1.50E+01	2.50E-01	2.50E-04
41J	2.27E+06	2.27E+00	3.79E-02	3.79E-05
41K	1.96E+06	1.96E+00	3.27E-02	3.27E-05
41L	0.00E+00	0.00E+00	0.00E+00	0.00E+00

Appendix Table 2. Summary of 2011 cultivated area (km²) and 2010 landings (lbs) for the three main species cultivated in South Puget Sound within WDFW aquaculture districts.

	Species					
	Pacific oyster		**Manila clam**		**Geoduck**	
District	Area	Landings	Area	Landings	Area	Landings
41A	NA	0	NA	0	NA	0
41B	0.29	0	0.431	0	46.895	0
41C	0.142	436	0.21	4,080	2.532	375,881
41D	1.018	27,606	1.069	146,756	0.862	120,655
41E	2.61	265,779	1.136	102,884	2.745	213,090
41F	2.187	223,086	1.772	2,814	14.677	165,359
41G	2.333	5,378	2.29	956,504	0.202	3,664
41H	6.652	415,032	6.676	2,356,049	1.63	147,729
41J	1.155	97,921	1.047	9,835	6.864	273,055
41K	0.384	10,036	0.403	0	0.199	2,873

Appendix Table 3. Summary of age (years) and size (either shell length (mm) or biomass (lbs)) at harvest by species.

Species	Harvest size	Harvest age (yr)	Source
Pacific oyster	100 mm	2	Kobayashi et al. 1997, Ruesink et al. 2006
Manila clam	50 mm	2–3	Ruesink et al. 2006, Toba et al. 2005
Geoduck	2 lbs	6	National Research Council 2010; Teri King, Washington Sea Grant, and P Sean McDonald, Univ. Washington School of Aquatic and Fishery Sciences, personal communication

Standing stock was converted from wet weight, W_{wet} (g), to dry weight, W_{dry}, using a relationship established for Pacific oysters (Kobayashi et al. 1997), as dry weight is a better predictor of filtration rate:

$$W_{dry} = 0.225W_{wet} - 0.193$$

Standing stock dry weight (in kg) was divided by cultivated area (km²) to determine standing stock density (kg km⁻²) within each WDFW aquaculture district (Table 1). Then the proportion of total cultivated area by species in South Puget Sound represented in each aquaculture district was calculated and these species-specific proportions were used to weight the final filtering capacity estimate across each district. Using this method to estimate standing stock density produces a minimum estimate, which is due to underreported landings and using the maximum potential value for cultivated area to calculate densities.

Clearance Rates

Filtration rate estimates based on published relationships to body size are available for geoduck, Pacific oyster and Manila clam (Table 4). Body size for these calculations was assumed to be same as average size at harvest. Geoduck clearance rate estimates were obtained from Davis (2010), measured from intertidal geoducks in Hood Canal, Puget Sound. These clearance rates were converted to $L\ h^{-1}\ g_{dry}^{-1}$. Geoduck weight was converted from wet to dry using Pacific oyster conversion equations (Kobayashi et al. 1997).

Appendix Table 4. Clearance rate calculations for Pacific oyster, Manila clam, and geoduck. W is expressed in g.

Species	Size	W_{wet}	W_{dry}	$L\ hr^{-1}\ indiv^{-1}$	$L\ hr^{-1}\ g_{wet}^{-1}$	$L\ hr^{-1}\ g_{dry}^{-1}$	Source
Pacific oyster	100 mm, 2.4 g_{dry}	11.52	2.4	3	0.260	1.250	Kobayashi et al. 1997, Ruesink et al. 2006
Manila clam	50 mm, 3.9 gwet	18.19	3.9	1	0.060	0.260	Ruesink et al. 2006, Solidoro et al. 2003
Geoduck	980 gwet		220.3	3	0.003	0.014	Davis 2014

LITERATURE CITED

Davis JP (2010) DNR Molluscan Study DRAFT Report: Clearance rate estimates in geoduck clams. Department of Natural Resources, Olympia, WA.

Kobayashi M, Hofmann EE, Powell EN, Klinck JM, Kusaka K (1997) A population dynamics model for the Japanese oyster, *Crassostrea gigas*. Aquaculture 149:285–321.

Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisehart LM (2006) Changes in productivity associated with four introduced species: ecosystem transformation of a 'pristine' estuary. Marine Ecology Progress Series 311:203–215.

Solidoro C, Canu DM, Rossi R (2003) Ecological and economic considerations on fishing and rearing of *Tapes phillipinarum* in the lagoon of Venice. Ecological Modelling 170:303–318.

Toba D, Dewey B, King T (2005) Small-scale clam farming for pleasure and profit in Washington. Washington Sea Grant, Seattle, Washington, 20 p.

Geographic Information System Approaches and Spatial Datasets Relevant to Shellfish Aquaculture Siting in Washington State

Dara Farrell, University of Washington (UW) Department of Mechanical Engineering; Jonathan CP Reum, Washington Sea Grant; P Sean McDonald, UW School of Aquatic and Fishery Sciences; Bridget E Ferriss, Washington Sea Grant; Chris J Harvey, NOAA Fisheries, Northwest Fisheries Science Center, Conservation Biology Division

ABSTRACT

Decisions on aquaculture siting increasingly require a spatial understanding of the physical, ecological, and social attributes of the coastal environment. Geographic information systems (GIS) offer an important framework for organizing spatial databases and performing spatial analyses. This section provides both an overview of a framework for applying GIS to evaluate spatial decisions regarding aquaculture siting and an inventory of key spatial datasets relevant to shellfish aquaculture in Washington State.

INTRODUCTION

In Washington State, shellfish aquaculture is culturally significant and economically important to coastal communities, and interest exists in further expanding the industry. However, shellfish aquaculture is often just one of several competing uses for the coastal environment, and local communities and governments may be confronted with complex questions regarding where and to what spatial extent aquaculture should be permitted (Frankic and Hershner 2003, Ross et al. 2013). At the same time, aquaculture expansion is also increasingly considered in relation to efforts to maintain the ecological integrity of coastal ecosystems and protect species of conservation or management concern (NRC 2010, Soto et al. 2008). Converting coastal habitat to aquaculture may bring some ecological benefits: for instance, possible reductions in phytoplankton, which may lower risk of hypoxic conditions (Dame 2011, Prins et al. 1998). However, this may potentially come at the exclusion of other uses or the loss of benthic habitats with significant ecological functions (Coen et al. 2011, NRC 2010).

Decisions on aquaculture siting increasingly require a spatial understanding of the physical, ecological, and social attributes of the coastal environment (Kapetsky et al. 2010, Ross et al. 2009). Poor site selection can result in decreased production, adverse ecosystem impacts, low economic performance, and conflict between growers and neighbors or the public (Kapetsky et al. 2010, Spencer 2008). However, compiling and analyzing data layers that correspond to criteria related to site feasibility can help growers and managers identify tradeoffs between potential production at a given site and ecological or social constraints. Geographic Information Systems (GIS) have emerged as an important tool for performing such analyses and have seen increased use in aquaculture spatial planning and site selection (Kapetsky et al. 2010, Nath et al. 2000, Ross et al. 2013). GIS offers a platform for organizing and assembling databases relevant to aquaculture siting and facilitates spatial analyses and map rendering, which can offer a powerful visual tools for supporting the decision-making process (Ross et al. 2009). To date, GIS has predominantly been applied to spatial planning issues related to finfish net pen or cage placement in coastal waters, but applications to shellfish aquaculture are growing (see review in Kapetsky et al. 2010).

In Washington State, shellfish growers and managers could potentially benefit from the application of GIS tools to the issue of site selection. To help stimulate and guide research efforts, this study provides both an overview of GIS approaches to evaluating spatial decisions regarding aquaculture siting and an inventory of key spatial datasets relevant to shellfish aquaculture in Washington State.

GIS USE IN AQUACULTURE PLANNING

Although spatial decision making can be approached in a number of ways, Nath et al. (2000) notes that the application of GIS for decision support in aquaculture planning ideally consists of seven phases: (1) identifying project objectives, (2) formulating specifications, (3) developing the analytical framework, (4) locating data sources, (5) organizing and manipulating data for input, (6) analyzing data and verifying outcomes, and (7) evaluating output (Figure 1). The scheme has met support elsewhere in the literature (Dempster and Sanchez-Jerez 2008, Kapetsky et al. 2010) and should be considered an iterative process. This study summarizes each phase with respect to the specific issue of identifying areas suitable for shellfish aquaculture.

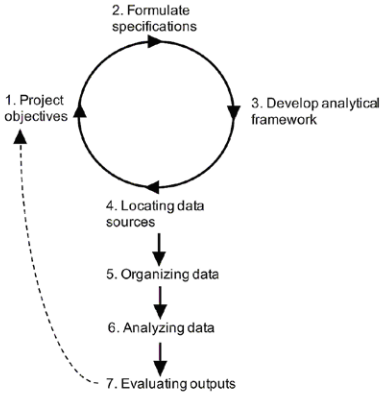


Figure 1. Overview of seven phases for applying geographic information systems in aquaculture planning decision support (adapted from Nath et al. 2000).

1. Identify Project Objectives

The first phase consists of conceptualizing the issue to be addressed with GIS. Articulating clear objectives and project goals will have bearing on the ultimate utility of the analysis to end users and, therefore, requires active participation and close involvement of multiple stakeholder groups (Soto et al. 2008). Until recently, this stage received limited treatment in the GIS literature, but it is among the most critical steps; carefully articulating the decision to be supported by GIS can yield time and cost savings by avoiding preparation of data layers that may go unused. In terms of the general issue of aquaculture siting, objectives will vary. For instance, the objective may be to identify sites optimal for aquaculture based primarily on production potential (Arnold et al. 2000, Buitrago et al. 2005). Alternatively, more comprehensive spatial planning efforts may view aquaculture as just one of several competing uses within the larger coastal environment (Ross et al. 2013). The goal may then include simultaneously optimizing the siting of aquaculture operations and zones for other industries and uses (Arnold et al. 2000, Hamouda et al. 2004, Klein et al. 2009).

2. Formulate Specifications

Once an overall understanding of project objectives has been developed, it may be helpful to develop a list of more functional specifications related to each objective. For instance, the project may require that the final GIS be interactive so that end users can explore alternate scenarios on their own (e.g., Alexander et al. 2012, Quan et al. 2001).

3. Develop Analytical Framework

Developing the analytical framework primarily concerns how project objectives identified in earlier steps will be met. In aquaculture siting studies, Multi-Criteria Evaluation (MCE) methods are often applied and generally entail calculating a habitat suitability index for aquaculture from parameters corresponding to several criteria (Longdill et al. 2008, Pérez et al. 2005, Radiarta et al. 2008, Silva et al. 2011, Simms 2002, Vincenzi et al. 2006; Figure 2). Various methods used are currently available for arriving at a habitat suitability index (Kapetsky and Aguilar-Manjarrez 2007, Malczewski 2006); this study highlights three of the most commonly used methods.

Additive Weighting

Under the simplest approach, data layers are first identified that correspond to criteria that enhance or detract from the level of suitability. Layers consisting of ordinal or continuous variables are then standardized to a common range (usually between 0 and 1). If each layer is assumed to contribute equally towards determining the value of a site for aquaculture, the values of the overlapping layers are summed, yielding a map conveying a suitability index (Malczewiski 1999). However, in most cases, criteria may be unequal in terms of importance. In these instances, criteria can be assigned relative weights, usually based on expert opinion. A habitat suitability index based on the weighted sum of overlapping layers is then calculated (e.g., Arnold et al. 2000, Buitrago et al. 2005).

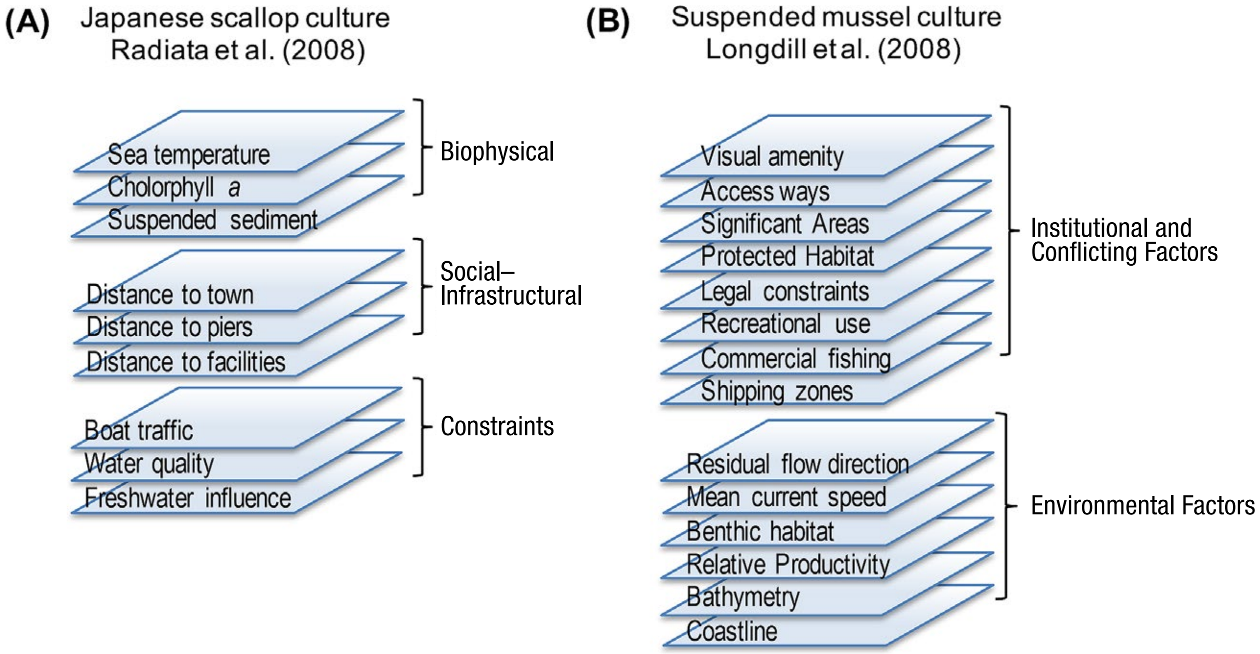


Figure 2. (A) Spatial layers corresponding to criteria included in an overlay analysis of habitat suitability for Japanese scallop *Mizuhopecten yessoensis* (Radiarta et al. 2008). Criteria were categorized into three submodels: biophysical, social-infrastructural, and constraints. (B) A set of criteria considered in the placement of mussel rafts in a coastal region in New Zealand (Longdill et al. 2008). Criteria were assigned to two categories: institutional and conflicting factors and environmental factors.

Parameter-Specific Suitability Functions

An elaboration of the additive weighting approach involves estimating parameter-specific suitability functions (PSSF), whereby each parameter is expressed in terms of a suitability index, usually defined on an arbitrary scale between 0 and 1 (0 corresponds to non-suitable conditions, 1 the most suitable conditions). PSSF may take linear or non-linear forms. As a nonlinear example, the PSSF of environmental variables (e.g., temperature, salinity) may be roughly bell-shaped, where the maximum value of 1 occurs at the physiological or survival optimum, and 0 occurs at values at extremes to both sides of the optimum (Vincenzi et al. 2006). Next, for each parameter, a new layer reflecting suitability based on the PSSF is calculated and the layer is assigned a weight reflecting its relative importance to overall habitat suitability. Rather than taking a weighted sum of the suitability layers to arrive at the habitat suitability index, a weighted geometric mean is instead calculated (Longdill et al. 2008, Vincenzi et al. 2006). The geometric mean implies that if a site is unsuitable with respect to one parameter (i.e., the PSSF value is 0), the overall habitat suitability index of the site is 0 regardless of the PSSF values of the other parameters (Vincenzi et al. 2006).

Analytic Hierarchy Process

The Analytic Hierarchy Process (AHP) was originally developed by Saaty (1980) and has been increasingly applied in spatial multi-criteria decision-making contexts (Malczewski 2006), including aquaculture siting (Radiarta et al. 2008). The method is based on the pairwise comparison of parameters included in the siting decision. All parameters are ranked against each other on a common continuous scale, and ratios conveying the level of importance of one parameter over another are obtained. The "importance ratios" are then organized into a matrix and cross-checked for consistency in rank order, and the weight of importance of each parameter is derived from the principal eigenvector of the matrix. A habitat suitability index can then be obtained by multiplying the normalized weights with the scaled value for each parameter and summing across all parameters (Malczewski 1999).

The approach also readily accommodates hierarchical criteria structures. For instance, site placement may depend on two broad criteria, economics and environment, which in turn may consist of several subcriteria corresponding to specific parameters. Under the AHP method, pairwise comparisons are performed separately at each level of the hierarchy. That is, the importance of economics relative to environment is specified, and similar pairwise comparisons are performed among subcriteria (parameters) within each criterion. The relative weights calculated for parameters within each criterion are then multiplied by the relative weights calculated for the respective broad criteria to form a vector of composite weights that represent the importance of parameters with respect to habitat suitability. Habitat suitability is then calculated by multiplying composite weights with the scaled parameter values and summing across all parameters as described previously (Radiarta et al. 2008). In general, the AHP method can be applied to criteria hierarchies consisting of any number of levels and can help reduce the conceptual complexity of the decision-making processes because only two parameters are considered at any give time (Malczewski 1999).

Considerations for Layer Weighting

All three approaches require subjective decisions regarding the weighting of layers, and how this is done requires careful thought based on the project objectives. Criteria weightings can be based on expert knowledge from a few individuals or information from the literature (e.g., Arnold et al. 2000, Vincenzi et al. 2006). Alternatively, many shellfish and aquaculture experts can be surveyed and asked to weight the relative importance of criteria for shellfish aquaculture siting (e.g., Buitrago et al. 2005, Longdill et al. 2008, Radiarta et al. 2008). As a third approach, a group decision-making process could be employed whereby stakeholders with an interest in the end product are brought together with the goal of reaching consensus on a weighting scheme (Malczewski 1999). If consensus is not possible, maps of habitat suitability corresponding to different stakeholder weighting schemes could be generated and compared for similarities to highlight regions of agreement (Malczewski 1999).

4. Identifying Data Sources

After an analytical framework has been developed, the data needed for the overall analysis must be identified (Nath et al. 2000). Ultimately, the criteria considered in any given analysis, and the manner in which they are grouped, will vary depending on the specific goals of the analysis, the types of aquaculture considered (species, cultivation method), interregional differences in regulatory constraints, and physical, ecological, and social conditions. For instance, in a habitat suitability evaluation for siting Japanese scallop culture, nine subcriteria were identified and organized into three broad criteria: biophysical, social-infrastructural, and constraints (Figure 2a; Radiarta et al. 2008). In contrast, an analysis of habitat suitability for mussel raft placement categorized 14 subcriteria into two broad criteria: institutional and conflicting factors and environmental factors (Figure 2b; Longdill et al. 2008). Although studies vary, some general patterns are apparent, with subcriteria typically falling into five broad criteria: physical, production, ecological, economic, and social considerations.

If data required for the analysis are lacking, project objectives should be revised or reevaluated altogether (Figure 1). If data resources have been identified and are sufficient for the analysis, they must then be sourced. In general, collecting primary (field) data is costly and time consuming (Nath et al. 2000). Instead, data are usually acquired through various secondary sources. For this study, investigators provided an overview of key datasets that may be relevant to aquaculture siting decisions in Washington State, their sources, and additional information on their spatial coverage, constraints, and limitations later in this section. The data search may uncover data gaps and issues that may require revising initial project objectives, specifications, or the analytical framework. Five broad data criteria are described as follows.

Physical

Physical criteria typically reflect constraints on the geographic extent of physically adequate habitat for a given type of cultivated species. The favorability of a habitat depends on the level of overlap between the physical requirements of the species and the physical properties of an area of interest. For example, water depth, exposure to air, temperature, siltation, substrate type, currents, and wave action may limit the feasibility of aquaculture at a given location (McKindsey et al. 2006, Spencer 2008). Similarly, physical properties that include chemical variables (e.g., salinity, concentrations of pollutants or dissolved oxygen) may influence survival and the potential geographic extent of aquaculture (McKindsey et al. 2006, Spencer 2008). In general, physical criteria provide a coarse indication of potential areas suitable for aquaculture production from which more specific site selections can be made for actual development (Ross et al. 2013).

Production

Production criteria correspond to harvest potential at a given site and include variables that influence shellfish growth rates. For filter feeding shellfish, growth is strongly influenced by food concentrations (phytoplankton, particulate organic matter), temperature, and stocking densities (Dame and Prins 1997), though other environmental variables (salinity, dissolved oxygen concentrations) can also be important (Spencer 2008). While spatial estimates of growth potential are possible using available modeling tools (e.g., Ferreira et al. 2007, Grant et al. 2007), they generally require considerable site-specific hydrodynamic, biological, and environmental information (McKindsey et al. 2006). If such data are available, site-specific estimates of growth potential can be estimated and included in siting decisions (Silva et al. 2011). However, in most regions, only some parameters relevant to growth potential are available. As a practical alternative, the variables themselves (e.g., temperature, food concentration, salinity) can be considered indicators of production potential and used as criteria for site suitability (Longdill et al. 2008, Radiarta et al. 2008, Vincenzi et al. 2006).

Ecological

Ecological siting criteria generally aim to minimize unacceptable ecological impacts including changes to ecological processes, services, species, populations, or communities in the environment (McKindsey et al. 2006, Ross et al. 2013). However, in practice, criteria will depend on society, which must choose specific components or processes of interest and identify limits for acceptable change (Byron et al. 2011, McKindsey et al. 2006), and this may be controversial (Lackey 2001). Specific criteria examples may include avoidance of ecologically important habitats (e.g., eelgrass beds) or areas where endangered or threatened species occur.

Economic

Economic criteria relate to investment demand or potential costs associated with sites. For instance, whether a site is near the base of operation, requires cost-prohibitive modifications (e.g., substrate graveling), or is in proximity to piers or land-based facilities may factor into the economic viability of a site (Spencer 2008). Other factors, including some biological variables, may also detract from a site. For instance, abundant predators, competitors, or disease may lead to high loss rates that may be costly to combat (Spencer 2008). Similarly, placement of farms in regions with frequent toxic algae blooms may reduce the availability of harvestable product that meets health standards.

Social

Social criteria include a potentially wide range of considerations. Criteria may include legal constraints on aquaculture development: for instance, coastal zoning plans at the city, county, and state level may expressly prohibit aquaculture development in some areas. Further, marine parks, protected habitats, tribal lands, designated shipping lanes, and military property may also restrict aquaculture (Kapetsky and Aguilar-Manjarrez 2007). A common goal in siting is to minimize potential impacts on other users of the coastal environment (Gilliland and Laffoley 2008). Therefore, criteria related to other activities may also be desirable. For instance, tourism, capture fisheries, and recreation (e.g., fishing, clamming, wind surfing, kayaking, sailing) are some of the activities that may conflict with aquaculture (Longdill et al. 2008, Perez et al. 2003, Silva et al. 2011). In addition, placement decisions may include social considerations such as proximity to public parks and the potential visibility of farms and their perceived impact on the scenic quality of coastlines (Outeiro and Villasante 2013, Radiarta et al. 2008).

5. Organizing and Manipulating Data

Once the data have been identified and collected, they should be organized into a database for use in the target GIS (Nath et al. 2000). This phase includes verifying data quality, consolidating and reformatting data and, in some cases, creating derived data layers. For instance, layers depicting wind-wave height and period can be derived using formulas that require spatial information on fetch distance and maximum wind speed and direction (Tallis et al. 2013). Alternatively, interpolation methods may be required to derive continuous spatial layers from point data obtained at discrete sampling stations (e.g., chlorophyll *a*, dissolved oxygen, or toxic algae concentrations; Vincenzi et al. 2006).

6. Analyzing Data

This phase includes generating habitat suitability maps and may entail performing overlay analyses based on multi-criteria evaluation methods selected in earlier planning phases (Hossain et. al 2009, Nath et. al 2000). Ultimately, details of the analysis will depend on the goals of the research.

7. Evaluating Outputs

The last phase involves evaluating the outputs of the analysis and ideally should involve end users, subject matter specialists, and the GIS analyst (Nath et al. 2000). Activities may include more detailed examination of individual project components together with any potential estimates of uncertainty or underlying assumptions (Ross et al. 2013). Initial project objectives should be compared with the outputs and updated, and the seven-step procedure reinitiated if necessary (Figure 1).

OVERVIEW OF WASHINGTON STATE DATA

To facilitate the potential use of GIS in aquaculture planning and site selection in Washington State waters, this study identified data layers and spatial products that might be useful in analyzing habitat suitability. In so doing, general data availability and needs were assessed to provide a starting point for those wishing to pursue aquaculture-relevant spatial analyses. Those setting out to perform spatial analysis should always directly examine the datasets they intend to use and judge for themselves their value and quality given the analysis goals. The study investigators primarily focused on identifying datasets with spatial coverage in Willapa Bay and South Puget Sound, as these areas are major regions of aquaculture development. However, they also noted when data coverage extended to other marine waters of the state. Extant data layers have been grouped under five themes: (1) current aquaculture and (2) physical, (3) production, (4) ecological, and (5) social considerations. General descriptions of each category are provided below and data sources are summarized in the appendix (p. 82).

1. Current Aquaculture

Considering the current spatial extent of aquaculture is important for identifying potential new sites. Currently, the best aquaculture siting data consist of point data for certified harvest locations (Figure 3), which are usually matched with additional site identification information (site tax parcel, state beach, or DNR-managed subtidal geoduck tract identification codes). The total area permitted for cultivation is noted for each location, but this may be significantly larger than the area actively cultivated because shellfish growers often leave some portion of the area fallow.

Aquaculture landings data are also available from the Washington Department of Fish & Wildlife (WDFW). Statistics are generated on a quarterly basis and landings are aggregated by WDFW shellfish harvest regions.

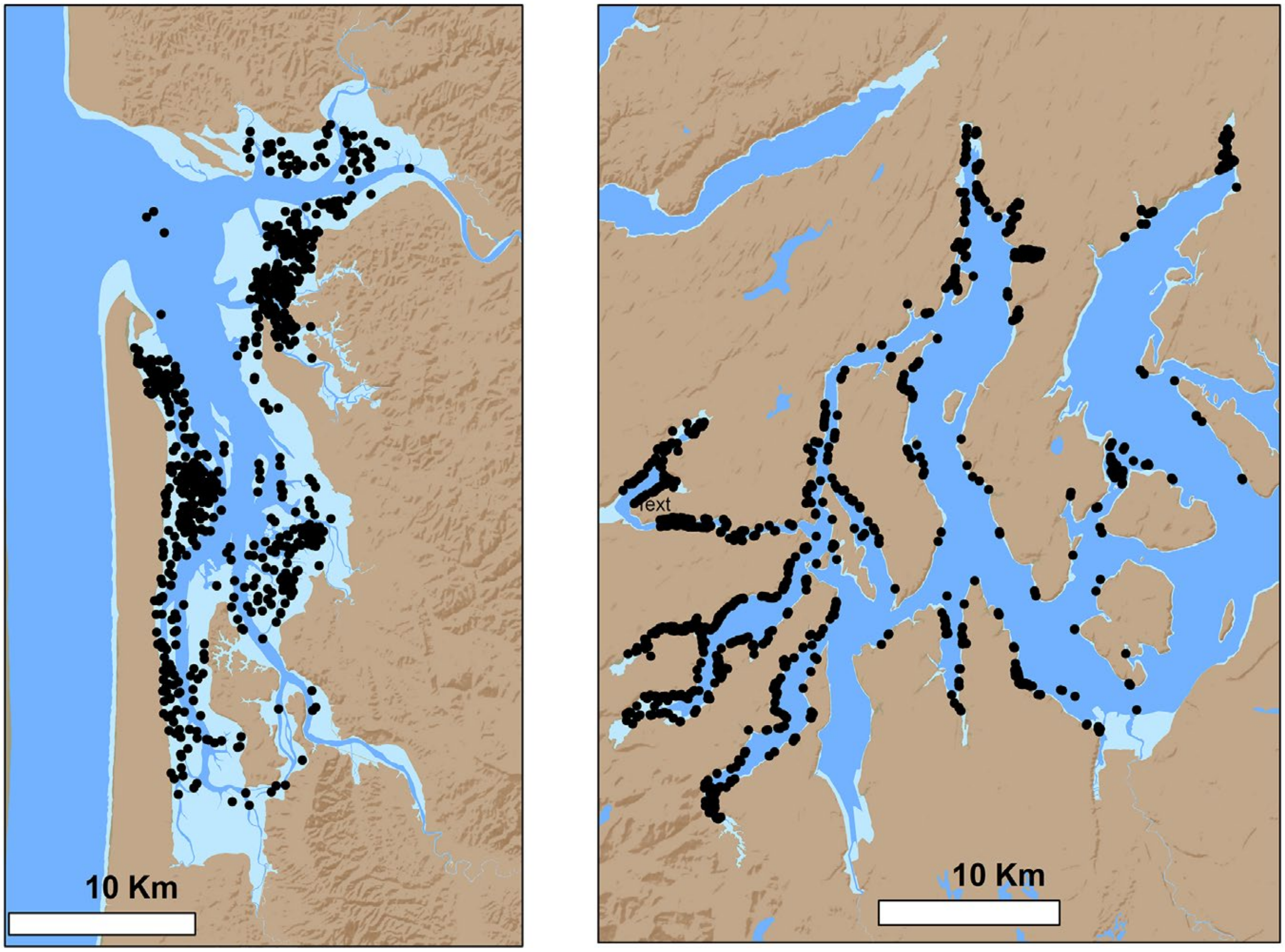


Figure 3. Locations of plots permitted for commercial shellfish harvest for Willapa Bay (left) and South Puget Sound (right); data from 2010, Washington State Department of Health.

2. Physical

Physical considerations include data layers that may inform whether a site is physically amenable to shellfish aquaculture, as well as layers that describe:

- bathymetry (via Digital Elevation Models (DEMs)),
- the presence of maritime infrastructure (e.g., over-water structures, ferry terminals, shipping lanes),
- boat traffic (e.g., shipping lanes), and
- regions with possible water quality issues (e.g., hazardous waste sites, state cleanup sites, proximity to combined sewage overflow and high stormwater outfalls; see appendix, p. 82).

Currently, publicly available DEMs from the U.S. Geological Survey and National Oceanic and Atmospheric Administration (NOAA) vary in terms of accuracy and resolution with regard to the intertidal depth band. For Puget Sound, Finlayson (2005) developed a continuous DEM that has been useful for a wide range of applications including oceanographic modeling. This DEM was derived from high resolution LIDAR and multibeam SONAR wherever these data were available. However, depth anomalies are apparent in some intertidal regions of the DEM (for example Totten Inlet in South Puget Sound). A layer identifying the source of data for each DEM value is available, which facilitates DEM updating with more accurate data if appropriate. Therefore, users should verify the data source for their study area if using this DEM for analysis in the intertidal band. For Willapa Bay, a field-verified, high resolution (5 square meters) DEM has been developed (B Dumbauld, United States Department of Agriculture, personal communication).

Aquaculture siting can also benefit from information on water properties such as temperature, salinity, and dissolved oxygen. Currently, the Washington State Department of Ecology (Ecology) samples marine water column properties on a monthly basis at stations located in Willapa Bay, Grays Harbor, and Puget Sound (5, 3, and 28 stations, respectively). Stations are generally located in waters deeper than 5 meters and separated by several kilometers. The utility of these data for inferring water conditions, particularly temperature and oxygen, in the nearshore may therefore be limited. For salinity, proxies such as distance to known freshwater point sources may be more useful (e.g., Radiarta et al. 2008) but may remain difficult to directly interpret. High-resolution oceanographic models may eventually offer an alternative resource for inferring nearshore water properties, but the current class of available oceanographic models of Puget Sound and the outer coast require additional development and testing against observations at the relevant and fine scale (e.g., Banas et al. 2007, Khangaonkar et al. 2012, Sutherland et al. 2011), though progress is being made (see Banas and Wei, p. 59, this report).

3. Production

As noted under the physical considerations, some data are limited to sampling stations that may not be informative about conditions in shallower, inshore waters (appendix, p. 82). In addition, data on potential food concentrations (based on phytoplankton standing stock densities) available from some of these same sampling stations have similar limitations. Although data on phytoplankton standing stock and production are meager, remote sensing methods may offer a promising avenue for characterizing fine-scale, spatiotemporal productivity patterns in Puget Sound and the outer coastal estuaries (see Box 1, Chlorophyll *a* Remote Sensing).

4. Ecological

Layers under this theme identify critical habitats (e.g., pocket estuaries, wetlands) and flora and fauna that are protected, threatened, or potentially sensitive to habitat loss or alteration. This information may be useful for identifying ecological tradeoffs or potential legal limitations when considering farm siting. The largest database on priority habitats and species is maintained by the WDFW (appendix, p. 82). The database includes layers corresponding to the general distribution of ecologically important or endangered taxa such as birds, marine mammals, fishes (e.g., salmon, forage fishes, pelagic fishes, bottom fishes) and the habitat types with which they associate. These layers do not represent exhaustive inventories and should be interpreted accordingly.

Eelgrass beds (*Zostera* spp.) form an ecologically important habitat type and can potentially be disturbed by shellfish aquaculture (Dumbauld et al. 2009). Information on the distribution of eelgrass in Washington State varies in quality and resolution. Specific resources include a relational database available through the Encyclopedia of Puget Sound that classifies coastline segments according to habitat type (Dethier 1990) and notes the presence of eelgrass (Dethier 2014). Coastline segments range in length from 18 to 38,337 meters and the dataset covers all Washington State coastlines. The National Land Cover Database offers a second resource on the potential distribution of eelgrass. In that dataset, satellite-based land imagery with a resolution of 30 square meters has been classified into different habitat types, and includes a “submerged aquatic vegetation” classification. The accuracy of the layer for depicting the extent of eelgrass has not been ground truthed. The current database (published 2011) corresponds to land cover patterns in 2006 and will not reflect any recent expansions or contractions in eelgrass habitat. In addition, the layer does not distinguish between native *Z. marina* and the non-native *Z. japonica*, which differ in terms of potential interaction with aquaculture (summarized in Reum et al. 2015).

Box 1

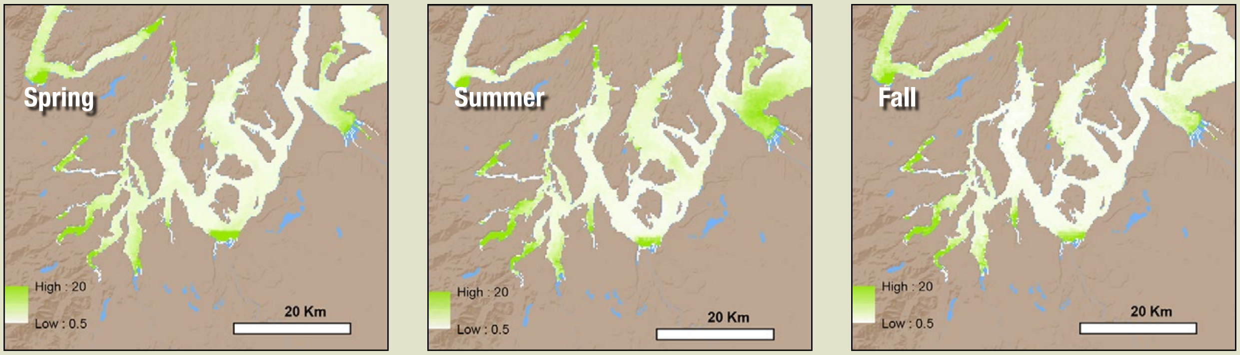
Chlorophyll a Remote Sensing

Phytoplankton is the main food source for filter-feeding shellfishes and directly influences individual growth rates and optimal farm stocking densities (Ferreira et al. 2007, Grant 1996). Therefore, shellfish production estimates are strongly dependent on ambient phytoplankton concentrations and, if farms are situated in low-productivity waters, harvests may fall short of levels required for economic viability. As a result, phytoplankton availability is an important criterion in siting decisions (Kapetsky and Aguilar-Manjarrez 2007). For some systems, there are hydrodynamic models that incorporate spatially resolved nutrient–phytoplankton–zooplankton dynamics, which can aid in estimating spatial primary production patterns (e.g., Grant et al. 2008). However, such models are data intensive, costly, and time-demanding. As a practical alternative, products derived from satellite-based remote-sensing technologies can offer estimates of synoptic surface chlorophyll a (Chl *a*) concentrations, which are correlated with phytoplankton biomass and can thus help inform siting decisions (Longdill et al. 2008, Radiarta et al. 2008).

In Puget Sound, efforts are currently underway to convert measurements of ocean color from a variety of sensors to estimates of surface Chl *a* concentrations (Sackmann 2014). Calibration of the estimates is facilitated by using in situ Chl *a* fluorescence measurements obtained from instrumentation installed onboard the passenger ferry *Victoria Clipper IV*. The satellite products provide surface Chl *a* concentration estimates at resolutions of 250 to 500 meters, and because images are taken at regular time intervals, seasonal or interannual variation in productivity can be examined. In the South Puget Sound subbasin, preliminary surface Chl *a* estimates reveal that the highest and most persistent concentrations generally occur in the smaller bays and inlets (Box 1 figure). While suspended sediment and bottom reflectance may impart considerable uncertainty into Chl *a* estimates for shallow areas, the relative patterns between deeper subbasins are more robust and suggest that seasonal variation in Chl *a* is minor relative to spatial variability (Box 1 figure).

Cloud cover and spurious measures of reflectance (due to confusion of land and water pixels) can also affect the accuracy of estimates from this method. However, further model refinement using in situ validation can help reduce prediction errors. Future research directions could include development of a real-time image processing workflow and a framework for disseminating results to shellfish growers and other end users.

Brandon Sackmann (Integral Consulting Inc), Jonathan Reum



Estimates of South Puget Sound surface chlorophyll a concentrations (milligrams per cubic meter) during spring, summer, and fall 2013 based on remote sensing.

5. Social

Layers under this theme may help identify areas that possibly conflict with other uses or which have already been zoned for other regulated uses. Social considerations may include areas with potential legal constraints: for instance, public parks, tribal lands, military areas, marine protected areas, and oyster reserves. In addition, municipality- and county-level marine shoreline management plans may further impose constraints on farm placement.

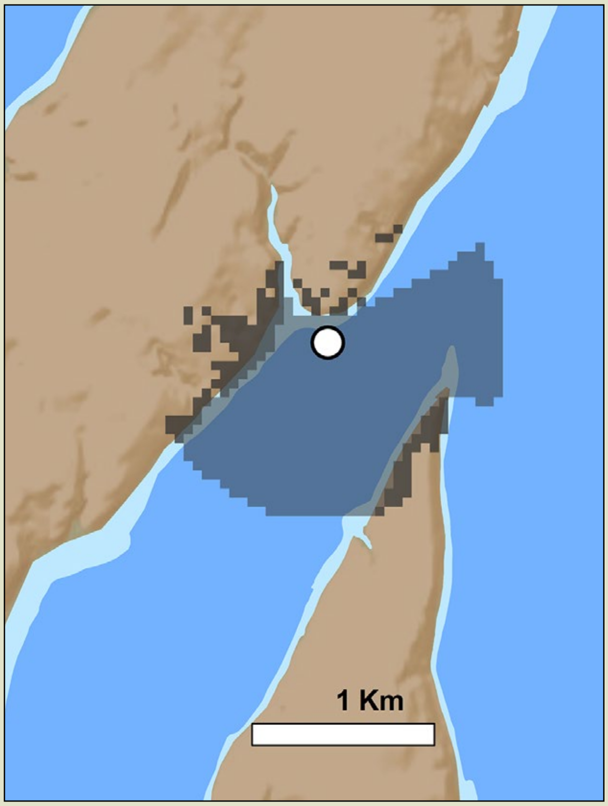
Further, there may be interest in avoiding sites near high densities of people or public parks to reduce the potential for poaching. Spatial layers of human density based on national census data are available as well as layers depicting public lands in Washington State. Alternatively, if shellfish farms are perceived as altering the aesthetic quality of coastlines, low visibility may be an important siting criteria. To help address this, The Natural Capital Project has developed the "Scenic Quality" tool, which estimates the visibility of geographic features (Tallis et al. 2013; Box 2, Viewshed). This tool can be used to generate data layers that relate the visibility of potential new farms to private homes, public parks, or any other location of interest, and it could easily be applied within a farm siting analysis.

Box 2

Viewshed

Potential social criteria relevant to aquaculture siting analyses include the level of visibility of proposed farms within viewsheds. Overall, the visibility of structures associated with farms in a viewshed depends on several factors including elevation (both of the viewer and farm), the level of exposure in relation to tide height, and the spatial extent and height of natural and man-made structures in the line of sight (e.g., trees, buildings). GIS-based tools are available that enable analysis of viewsheds given different scenarios of aquaculture development (Outeiro and Villasante 2013, Puniwai et al. 2014), and they can generate layers that could be incorporated into spatial multi-criteria decision support frameworks for farm siting (Malczewski 1999).

Widely used GIS software packages such as ArcGIS, QGIS, and GRASS facilitate viewshed analyses through built-in tools or plugins. The Scenic Quality tool developed by The Natural Capital Project (Tallis et al. 2013) is designed especially for analyzing viewsheds in the marine nearshore environment. The package contains built-in raster layers for population density and elevation, but these may have insufficient spatial resolution, depending on the goals and spatial scale of the intended analysis. However, analysts can easily supply their own elevation and population density data layers and include additional layers to account for trees, buildings, or other features that may obstruct views. The output from the Scenic Quality tool includes a raster layer that classifies the visual quality of the analysis region (from no visual impact to very high visual impact) and provides additional summary metrics. To help illustrate the approach, the Scenic Quality tool was used to estimate the area over which a hypothetical farm could be viewed at a location in South Puget Sound (Box 2 figure). In this example analysis, the Finlayson (2005) DEM was modified to reflect forested areas using a surrogate canopy raster created using the National Land Cover Database. Areas within the DEM with more than 50% tree coverage were assigned an additional elevation of 20 meters. Populations residing in forested areas (greater than 50% tree coverage) were assumed to not have water views; they were consequently removed from the population density data layer. The area from which structure at the hypothetical farm may be visible at low-tide during daylight hours was depicted (Box 2 figure).



An example calculation of the area from which a proposed farm structure (open circle symbol) may be visible using the Scenic Quality tool (Tallis et al. 2013). The dark shading surrounding open symbol corresponds to areas from which the site may be visible.

Currently, several challenges exist for implementing viewshed analyses related to intertidal aquaculture in Washington State and Puget Sound in particular. Foremost, high- resolution digital elevation data of the intertidal is critical, and data of sufficient accuracy are not available in many regions. This is especially important because structure visibility will vary with tidal exposure and such calculations will be sensitive to relatively small inaccuracies in bathymetry. Next, visibility will depend on the type of farm structure, and the analysis requires the subjective weighting of visibility. The visibility of a newly planted geoduck plot with anti-predator netting likely differs from that of an on-bottom oyster bed. Distinguishing differences in visibility between the farms is possible using the Scenic Quality tool, though this requires a subjective choice in the relative difference in visibility “weight.” This could potentially be approached by assigning weights based on input from multiple stakeholder groups. Finally, estimates of visibility would benefit from more extensive cataloguing of use patterns in coastal recreational areas to better estimate the number of persons with line of sight of proposed new sites.

Dara Farrell, Jonathan Reum

CONCLUSIONS

In the last two decades, GIS has emerged as an important tool for supporting aquaculture siting decisions but remains underutilized in Washington State. GIS can help develop a useful framework for organizing spatial data resources and a powerful platform for performing analyses that can inform the decision-making process (Arnold et al. 2000, Longdill et al. 2008, Radiarta et al. 2008). Currently, various data resources could feed directly into an assessment of aquaculture feasibility, which might help inform long-term planning. In addition, tools are available that can generate data layers particularly relevant to issues in Washington State such as visibility, and potential data sources that, with further refinement and support, may offer valuable information for shellfish growers (e.g., remotely sensed sea surface estimates of Chl *a*). The dataset inventory provided by this study is not exhaustive, and other available data may be valuable depending on the question at hand. County-maintained GIS repositories and geospatial data clearinghouses for Washington State data are good starting points (several are indicated herein), and many also provide other suggested resources. Not all data may be maintained by the respective agencies and more current records may be available from the data originator.

GIS Repositories and Geospatial Data Clearinghouses for Washington State

Washington State Department of Natural Resources GIS Data Center: This site features layers related to natural resources such as aquatic, habitat, climatology, geology, forest practices, hydrography, and natural heritage.
http://www.dnr.wa.gov/programs-and-services/geology-and-earth-resources

Ecology's spatial dataset: This includes data related to air and water quality, public beaches, tribal lands, and pollution sources.
http://www.ecy.wa.gov/services/gis/data/data.htm

Washington State Geospatial Data Archive: This is maintained by The Map Collection & Cartographic Information Services, University of Washington (UW) Libraries, and also contains selected non-Washington geospatial datasets created by students and researchers at the UW. Some datasets are restricted to persons affiliated with the UW, though many are public domain datasets.
http://wagda.lib.washington.edu

Washington State Department of Health: This agency has data pertinent to commercial and recreational shellfish harvesting including recreational shellfish beaches and closed beaches.
https://fortress.wa.gov/doh/eh/maps/OSWPViewer/index.html

NOAA's Digital Coast site: This site includes data on physical and oceanographic variables, elevation, marine habitats and species, climatology, and marine planning data such as usage, jurisdictions, and boundaries.
http://coast.noaa.gov/dataregistry/search/collection

Washington Marine Spatial Planning Data Catalog: The catalog primarily contains datasets relevant to activities and physical and environmental variables on the outer Washington coast.
http://www.msp.wa.gov

Washington State Geospatial Portal: This portal links users to GIS data layers and other geospatial information and products produced and maintained by state agencies such as the WDFW.
http://geography.wa.gov/data-products-services/data/data-catalog

Washington State Department of Transportation (WSDoT) GeoData Distribution Catalog: This catalog includes data layers produced by WSDOT related to transportation routes (including ferry routes).
http://www.wsdot.wa.gov/Mapsdata/GeoDataCatalog/default.htm

Encyclopedia of Puget Sound: This online encyclopedia is a growing compilation of data related to Puget Sound with some real-time data available via their online viewer.
http://www.eopugetsound.org/maps

LITERATURE CITED

Alexander KA, Janssen R, Arciniegas G, O'Higgins TG, Eikelboom T, Wilding TA (2012) Interactive Marine Spatial Planning: siting tidal energy arrays around the Mull of Kintyre. PLoS ONE 7:e30031.

Arnold W, Norris H, Berrigan M (1996) Lease site considerations for hard clam aquaculture in Florida. Journal of Shellfish Research 15:478-479.

Arnold WS, White MW, Norris HA, Berrigan ME (2000) Hard clam (*Mercenaria* spp.) aquaculture in Florida, USA: geographic information system applications to lease site selection. Aquacultural Engineering 23:203-231.

Banas NS, Hickey BM, Newton JA, Ruesink JL (2007). Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. Marine Ecology Progress Series 341:123-139.

Buitrago J, Rada M, Hernández H, Buitrago E (2005) A single-use site selection technique, using GIS, for aquaculture planning: choosing locations for mangrove oyster raft culture in Margarita Island, Venezuela. Environmental Management 35:544-556.

Byron C, Link J, Costa-Pierce B, Bengtson D (2011) Modeling ecological carrying capacity of shellfish aquaculture in highly flushed temperate lagoons. Aquaculture 314:87-99.

Coen LD, Dumbauld B, Judge M (2011) Expanding shellfish aquaculture: a review of the ecological services provided by and impacts of native and cultured bivalves in shellfish-dominated ecosystems. Chapter 9 in Shumway SE (ed), Shellfish Aquaculture and the Environment. Wiley-Blackwell, Danvers, MA.

Dame RF (2011) Ecology of Marine Bivalves: an Ecosystem Approach. CRC Press

Dame RF, Prins TC (1997) Bivalve carrying capacity in coastal ecosystems. Aquatic Ecology 31:409-421.

Dempster T, Sanchez-Jerez P (2008) Aquaculture and coastal space management in Europe: an ecological perspective. In Holmer M, Black K, Duarte CM, Marba N, Karakassis I (eds), Aquaculture in the Ecosystem, Springer, pp. 87-116.

Dethier MN (1990) A marine and estuarine habitat classification system for Washington State. Washington Natural Heritage Program, Washington Department of Natural Resources, Olympia, Washington, 56 p.

Dethier MN (last modified 2014) Shoreline habitat classifications. Encyclopedia of Puget Sound. Available at *http://www.eopugetsound.org/habitats/shore-types*.

Dumbauld BR, Ruesink JL, Rumrill SS (2009) 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. Aquaculture 290:196-223.

Ferreira J, Hawkins A, Bricker S (2007) Management of productivity, environmental effects and profitability of shellfish aquaculture—the Farm Aquaculture Resource Management (FARM) model. Aquaculture 264:160-174.

Finlayson D (last modified December 24, 2005) Combined bathymetry and topography of the Puget Lowland, Washington State. University of Washington. Available at *http://www.ocean.washington.edu/data/pugetsound/.*

Frankic A, Hershner C (2003) Sustainable aquaculture: developing the promise of aquaculture. Aquaculture International 11:517-530.

Grant J (1996) The relationship of bioenergetics and the environment to the field growth of cultured bivalves. Journal of Experimental Marine Biology and Ecology 200(1):239-256.

Grant J, Curran KJ, Guyondet TL et al. (2007) A box model of carrying capacity for suspended mussel aquaculture in Lagune de la Grande-Entrée, Iles-de-la-Madeleine, Québec. Ecological modelling 200(1-2):193-206.

Gilliland P, Laffoley D (2008) Key elements and steps in the process of developing ecosystem-based marine spatial planning. Marine Policy 32(5):787-796.

Hamouda L, Kilgour DM, Hipel KW (2004) Strength of preference in the graph model for conflict resolution. Group Decision and Negotiation 13(5):449-462.

Hossain MS, Chowdhury SR, Das NG, Sharifuzzaman SM, Sultana A (2009). Integration of GIS and multicriteria decision analysis for urban aquaculture development in Bangladesh. Landscape and Urban Planning 90(3):119-133.

Kapetsky J, Aguilar-Manjarrez J, Soto D (2010) Status and potential of spatial planning tools, decision-making and modelling in implementing the ecosystem approach to aquaculture. In Aguilar-Manjarrez J, McDald Kapetsky J, Soto D (eds), The Potential of Spatial Planning Tools to Support the Ecosystem Approach to Aquaculture. Proceedings of the United Nations Expert Workshop, November 19-21, 2008, Rome, No. 17. Fisheries and Aquaculture Department, FAO Rome, p. 19-21.

Kapetsky JM, Aguilar-Manjarrez J (2007) Geographic information systems, remote sensing and mapping for the development and management of marine aquaculture. FAO Fisheries Technical Paper No. 458, Fisheries and Aquaculture Department, FAO, Rome, 125 p.

Khangaonkar T, Sackmann B, Long W, Mohamedali T, Roberts M (2012) Simulation of annual biogeochemical cycles of nutrient balance, phytoplankton bloom (s), and DO in Puget Sound using an unstructured grid model. Ocean Dynamics 62(9):1353-1379.

Klein CJ, Steinback C, Watts M, Scholz AJ, Possingham HP (2009) Spatial marine zoning for fisheries and conservation. Frontiers in Ecology and the Environment 8:349-353.

Lackey RT (2001) Values, policy, and ecosystem health: options for resolving the many ecological policy issues we face depend on the concept of ecosystem health, but ecosystem health is based on controversial, value-based assumptions that masquerade as science. BioScience 51:437-443.

Longdill PC, Healy TR, Black KP (2008) An integrated GIS approach for sustainable aquaculture management area site selection. Ocean & Coastal Management 51:612-624.

Malczewski J (1999) GIS and Multicriteria Decision Analysis. John Wiley & Sons, New York.

Malczewski J (2006) GIS-based multicriteria decision analysis: a survey of the literature. International Journal of Geographical Information Science 20:703-726.

McKindsey CW, Thetmeyer H, Landry T, Silvert W (2006) Review of recent carrying capacity models for bivalve culture and recommendations for research and management. Aquaculture 261:451-462.

Nath SS, Bolte JP, Ross LG, Aguilar-Manjarrez J (2000) Applications of geographical information systems (GIS) for spatial decision support in aquaculture. Aquacultural Engineering 23:233-278.

NRC (National Research Council) (2010) Ecosystem Concepts for Sustainable Bivalve Mariculture. National Academies Press, Washington, D.C.

Outeiro L, Villasante S (2013) Linking salmon aquaculture synergies and trade-offs on ecosystem services to human wellbeing constituents. AMBIO 42:1022-1036.

Perez O, Telfer T, Ross L (2003) Use of GIS-based models for integrating and developing marine fish cages within the tourism industry in Tenerife (Canary Islands). Coastal Management 31:355-366.

Pérez OM, Telfer TC, Ross LG (2005) Geographical information systems-based models for offshore floating marine fish cage aquaculture site selection in Tenerife, Canary Islands. Aquaculture Research 36:946-961

Prins TC, Smaal AC, Dame RF (1998) A review of the feedbacks between bivalve grazing and ecosystem processes. Aquatic Ecology 31:349-359.

Puniwai N, L Canale, M Haws, J Potemra, C Lepczyk, S Gray (2014) Development of a GIS-based tool for aquaculture siting. ISPRS International Journal of Geo-Information 3:800-816.

Quan J, N Oudwater, J Pender, A Martin (2001) GIS and participatory approaches in natural resources research. Socio-economic methodologies for natural resources research. Best practice guidelines. Natural Resources Institute, Chatham, UK, 36 p.

Radiarta IN, Saitoh S-I, Miyazono A (2008) GIS-based multi-criteria evaluation models for identifying suitable sites for Japanese scallop (*Mizuhopecten yessoensis*) aquaculture in Funka Bay, southwestern Hokkaido, Japan. Aquaculture 284:127-135.

Reum JCP, Ferriss BE, McDonald PS, Farrell DM, Harvey CJ, Klinger T, Levin PS (2015) Evaluating community impacts of ocean acidification using qualitative network models. Marine Ecology Progress Series 536:11-24.

Ross L, Telfer TC, Falconer L et al. (2013) Carrying capacities and site selection within the ecosystem approach to aquaculture. In Ross LG, Telfer TC, Falconer L (eds) Site Selection and Carrying Capacities for Inland and Coastal Aquaculture. Proceedings of the United Nations Expert Workshop, December 6-8, 2010, Rome, No. 17. FAO Fisheries an Aquaculture Department, Rome, p. 19-46.

Ross LG, Handisyde N, Nimmo D-C, Burnell G, Allan G (2009) Spatial decision support in aquaculture: the role of geographical information systems and remote sensing. In Burnell G, Allan, G (eds) New Technologies in Aquaculture: Improving Production Efficiency, Quality and Environmental. CRC Press, Boca Raton, Florida, p. 707-749.

Saaty TL (1980) The Analytic Hierarchy Process: Planning, Priority Setting, Resource Allocation. McGraw-Hill, New York, 531 p.

Sackmann BS (2014) Optics from ferries as ground truth for satellite ocean color products in Puget Sound. Poster presentation and extended abstract, Ocean Optics XXII, October 26-31, 2014, Portland, ME.

Silva C, Ferreira J, Bricker S, DelValls T, Martín-Díaz M, Yáñez E (2011) Site selection for shellfish aquaculture by means of GIS and farm-scale models, with an emphasis on data-poor environments. Aquaculture 318:444-457.

Simms A (2002) GIS and aquaculture: assessment of soft-shell clam sites. Journal of Coastal Conservation 8:35-48.

Soto D, Aguilar-Manjarrez J, Brugère C et al. (2008) Applying an ecosystem-based approach to aquaculture: principles, scales and some management measures. In Soto D, Aguilar-Manjarrez J, Hishamunda N (eds) Building an Ecosystem Approach to Aquaculture. Proceedings of the United Nations Expert Workshop, May 7-11, 2007, Palma de Mallorca, Spain, No. 14. FAO Fisheries an Aquaculture Department, Rome, p. 15-27.

Spencer B (2008) Molluscan Shellfish Farming. John Wiley & Sons, London.

Tallis HT, Ricketts T, Guerry AD (2013) InVEST 2.6.0 User's Guide. The Natural Capital Project, Stanford, CA.

Vincenzi S, Caramori G, Rossi R, De Leo GA (2006) A GIS-based habitat suitability model for commercial yield estimation of *Tapes philippinarum* in a Mediterranean coastal lagoon (Sacca di Goro, Italy). Ecological Modelling 193:90-104.

Appendix

DATA LAYERS RELEVANT TO AQUACULTURE SITING IN WASHINGTON STATE

Apendix Table 1. Description of extant data layers that may be relevant to aquaculture siting issues in Washington State. In addition, some useful tools for calculating relevant data layers are indicated. Data were categorized according to five themes: current aquaculture areas and landings, and physical, production, ecological, and social constraints. Abbreviations: DNR, Washington Department of Natural Resources; DOH, Washington State Department of Health; Ecology, Washington State Department of Ecology; NOAA, National Oceanic and Atmospheric Administration; OFM, Office of Financial Management; PSI, Pacific Shellfish Institute; RCO, Washington State Recreation and Conservation Office; USDOI, U.S. Department of Interior; USFWS, U.S. Fish and Wildlife Service; USGS, U.S. Geological Survey; WDFW, Washington Department of Fisheries & Wildlife; WSDOT; Washington State Department of Transportation.

Variable	Dataset description	Data source	Spatial coverage
	CURRENT AQUACULTURE AREAS AND LANDINGS		
Commercial shellfish harvest locations	These are point data for certified harvest locations with descriptive data that includes area permitted for cultivation and the species. Sites corresponding to privately owned tax parcels are assumed to reflect commercial aquaculture locations.	DOH; available upon request	State-wide
Shellfish landings, aggregated to commercial shellfish growing regions	Tabulated landings aggregated to commercial shellfish growing areas. Landings available by species and on a quarterly basis. This is possibly an incomplete picture of total landings owing to underreporting.	WDFW; available upon request	State-wide
	PHYSICAL		
Intertidal habitat (aquatic land parcels)	The aquatic land parcel data layer indicates the spatial extent of intertidal and subtidal habitats. The layer contains ownership information and physical and legal characteristics for each aquatic parcel.	DNR; *https://fortress.wa.gov/dnr/adminsa/gisdata/datadownload/state_aqparcel.zip*	State-wide
Digital elevation model	The most comprehensive digital elevation model (DEM) for the inland waters of Washington is Finlayson (2005). The data layer synthesizes numerous DEMs, with varying spatial resolution to yield a continuous surface spanning Puget Sound and surrounding watersheds. Measurement of intertidal depths is challenging in general, and depth accuracy of the DEM may be low in regions (e.g., anomalies are present in intertidal habitats in Totten Inlet, South Puget Sound).	Finlayson (2005)	Puget Sound, Straight of Juan de fuca
Digital elevation model	Relevant sources include: The USGS National Elevation dataset; NOAA's Digital Coast site; Olympic Natural Resource Center DEM mosaic (combines data from NOAA, USDA and USGS).	*http://ned.usgs.gov/* *http://www.coast.noaa.gov/* *http://www.onrc.washington.edu/clearinghouse*	Willapa Bay
Presence of overwater structures	Overwater structures in marine waters of Washington State: location and footprint of overwater structures such as docks, bridges, floats, structural support fill, and other structures such as floating homes.	DNR; *https://fortress.wa.gov/dnr/adminsa/gisdata/datadownload/wa_overwater_marine.zip*	State-wide
Ferry terminals	This layer depicts the locations of ferry terminals in Washington State. Only ferry terminals that are directly adjacent to a Washington State highway routes are available.	DOT; *ftp://ftp.wsdot.wa.gov/gis/GeoDataDistribution/Maps/24k/DOT_Cartog/ferrytermspubpriv.zip*	State-wide
Shipping lanes	Marine Cadastre/Navigation and Marine Transportation. Online at http://marinecadastre.gov.	NOAA; *ftp://ftp.csc.noaa.gov/pub/MSP/ShippingFairwaysLanesandZones.zip*	State-wide
Ferry routes	Routes of vessels providing scheduled, public car ferry service in the waters of Washington State are depicted as linear features. Known private, provincial, tribal, and passenger-only ferry services are also shown.	WSDOT; *ftp://ftp.wsdot.wa.gov/gis/GeoDataDistribution/Maps/24k/DOT_Cartog/ferry.zip*	State-wide

continued on next page

Appendix Table 1 · continued

Variable	Dataset description	Data source	Spatial coverage
PHYSICAL continued			
Hazardous waste sites, state cleanup sites, superfund sites	Facilities database (updated every Sunday)	Ecology; *ftp://www.ecy.wa.gov/gis_a/enviro/FacilitySite.gdb.zip*	State-wide
Proximity to combined sewage overflow (CSO) and highway stormwater outfalls	Point locations of CSO and outfalls	People for Puget Sound (via WDFW)	Puget Sound counties
Water properties (temperature, salinity, oxygen)	Ecology, marine monitoring stations	Ecology; *http://www.ecy.wa.gov/programs/eap/mar_wat/pdf/stationinfo.html*	Willapa Bay, Grays Harbor, Puget Sound
Shellfish biotoxin closure zones	Biotoxin Closure Zones: this dataset defines areas of marine waters that are managed for shellfish biotoxin closures.	DOH; *ftp://ftp.doh.wa.gov/geodata/layers/closurezones.zip*	State-wide
	PRODUCTION		
Water properties (temperature, salinity, oxygen)	Ecology, marine monitoring stations	Ecology; *http://www.ecy.wa.gov/programs/eap/mar_wat/pdf/stationinfo.html*	Willapa Bay, Grays Harbor, Puget Sound
Chlorophyll *a*	Ecology, marine monitoring stations	Ecology; *http://www.ecy.wa.gov/programs/eap/mar_wat/pdf/stationinfo.html*	Willapa Bay, Grays Harbor, Puget Sound
	ECOLOGY		
Protected habitats and species	Protected Habitats and Species Generalized Digital Data. Generalized distribution of ecologically important or endangered taxa: birds, marine mammals, fishes (salmon, forage fishes, pelagic fishes, bottom fishes), or the habitat type with which they are associated. Information on specific locations of some fish and wildlife species is considered sensitive and such data are removed from non-sensitive layers that might be of sufficient resolution to reveal these locations. More detailed analysis may require field investigations and additional assistance may be needed in interpreting and applying information from the database, depending on the species and area being considered.	WDFW; *http://wdfw.wa.gov/mapping/phs/*	State-wide
Summer and winter bird survey data	Puget Sound Assessment and Monitoring Program (PSAMP) Geodatabase. Winter and summer bird survey data for select species.	WDFW; *available upon request*	Puget Sound
Eelgrass	This layer provides shore type descriptions, physical attributes, and related species lists (including eelgrass species) that align spatially with classifications adapted from the Washington State ShoreZone Inventory linear shoreline data. More information is available at *http://www.eopugetsound.org/habitats/shore-types*.	DNR; *https://erma.noaa.gov/northwest/erma.html#/x=-120.95568&y=46.09146&z=7&layers=16+7942+1276+11371+1284*	State-wide
Submerged aquatic vegetation	U.S. Geological Survey, 20140331, NLCD 2006 Land Cover (2011 Edition): U.S. Geological Survey, Sioux Falls, SD. These data are compiled from the National Land Coverage Database. Submerged aquatic vegetation may be useful as a surrogate for an eelgrass location layer for certain locations. This layer has not been ground truthed for accuracy. More information is available at *http://www.mrlc.gov*.	USDOI, USGS; *http://viewer.nationalmap.gov/basic/*	State-wide
Proximity to pocket estuaries	Point locations of pocket estuaries	NOAA; *https://erma.noaa.gov/northwest/erma.html#/x=-120.95568&y=46.09146&z=7&layers=16+7942+1276+11371+1284*	unknown
Proximity to wetlands	National Wetlands Inventory	USFWS; *http://www.fws.gov/wetlands/index.html*	State-wide
Impaired or threatened water bodies	2012 Water Quality Assessment: Washington areas reported to the Environmental Protection Agency as impaired water under the Clean Water Act.	Ecology; *ftp://www.ecy.wa.gov/gis_a/environment/303d12.gdb.zip*	State-wide

continued on next page

Appendix Table 1 • continued from previous page

Variable	Dataset description	Data source	Spatial coverage
	SOCIAL		
Tribal Lands	Tribal lands: this dataset describes Native American ceded tribal lands in Washington State.	Ecology; *ftp://www.ecy.wa.gov/gis_a/boundaries/tribal.zip*	State-wide
Military/naval waters	Military and naval waters are indicated in the Aquatic Land Parcel layer. More generally, the layer contains ownership information and physical and legal characteristics of Washington State's aquatic land ownership records. For example, this layer may be used to define military or naval waters.	DNR; *https://fortress.wa.gov/dnr/adminsa/gisdata/datadownload/state_aqparcel.zip*	State-wide
Protected areas (wildlife refuge, state/county parks)	Public Lands Inventory database	Ecology; *ftp://www.ecy.wa.gov/gis_a/boundaries/tribal.zip*	State-wide
Marine Protected Areas Inventory	The Marine Protected Areas Inventory (MPA Inventory): geospatial database designed to catalog and classify marine protected areas within U.S. waters.	NOAA; *http://marineprotectedareas.noaa.gov/pdf/helpful-resources/inventory/mpa_inventory_2013_public_gdb.zip*	State-wide
Marinas/Boat launches and moorages	Motorized boat launches of Washington State: this dataset contains geographic point data for motorized boat launches found to be open to the public in Washington State at the time of the field inventory (1997). Moorage facilities of Washington State: this dataset is based on a comprehensive field inventory of large boat facilities conducted by the Washington State Recreation and Conservation Office in 2000.	RCO; *http://www.rco.wa.gov/data/RCOBoatFacilities.gdb.zip*	State-wide
Oyster reserves	Aquatic Land Parcel contains ownership information and physical and legal characteristics of Washington State's aquatic land ownership records: this layer is used to show oyster reserves.	DNR; *https://fortress.wa.gov/dnr/adminsa/gisdata/datadownload/state_aqparcel.zip*	State-wide
Scenic quality	The Scenic Quality model employs viewshed analysis to estimate the visibility of new nearshore or offshore features. The model generates maps that can identify the visual footprint of offshore development plans and highlight coastal areas more likely to be directly affected by additions to the seascape. Requires data layer on density of people. Can also be used to evaluate scenic quality from the vantage of public parks and beaches.	*Natural Capital Project, Scenic Quality Tool v3.01;* *program available at: http://naturalcapitalproject.org/InVEST.html*	N/A
Human densities	GRUMP - Global Rural-Urban Mapping Project. Population data estimates are provided for 1990, 1995, and 2000, and projected (in 2004, when GPWv3 was released) to 2005, 2010, and 2015.These globally available population data do not account for seasonal or daily users in an area.	*http://sedac.ciesin.columbia.edu/data/collection/gpw-v3*	State-wide

LITERATURE CITED

Finlayson D (last modified December 24, 2005) Combined bathymetry and topography of the Puget Lowland, Washington State. University of Washington. Available online: *http://www.ocean.washington.edu/data/pugetsound/*.

Washington Sea Grant
College of the Environment
University of Washington
3716 Brooklyn Avenue N.E.
Seattle, WA 98105-6716

206.543.6600
seagrant@u.washington.edu
wsg.washington.edu