

THE OFFICIAL MAGAZINE OF THE OCEANOGRAPHY SOCIETY

Oceanography

CITATION

Barton, A., G.G. Waldbusser, R.A. Feely, S.B. Weisberg, J.A. Newton, B. Hales, S. Cudd, B. Eudeline, C.J. Langdon, I. Jefferds, T. King, A. Suhrbier, and K. McLaughlin. 2015. Impacts of coastal acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented in response. *Oceanography* 28(2):146–159, <http://dx.doi.org/10.5670/oceanog.2015.38>.

DOI

<http://dx.doi.org/10.5670/oceanog.2015.38>

COPYRIGHT

This article has been published in *Oceanography*, Volume 28, Number 2, a quarterly journal of The Oceanography Society. Copyright 2015 by The Oceanography Society. All rights reserved.

USAGE

Permission is granted to copy this article for use in teaching and research. Republication, systematic reproduction, or collective redistribution of any portion of this article by photocopy machine, reposting, or other means is permitted only with the approval of The Oceanography Society. Send all correspondence to: info@tos.org or The Oceanography Society, PO Box 1931, Rockville, MD 20849-1931, USA.

Impacts of Coastal Acidification on the **Pacific Northwest Shellfish Industry** and Adaptation Strategies Implemented in Response

By Alan Barton, George G. Waldbusser, Richard A. Feely,
Stephen B. Weisberg, Jan A. Newton, Burke Hales,
Sue Cudd, Benoit Eudeline, Chris J. Langdon, Ian Jefferds,
Teri King, Andy Suhrbier, and Karen McLaughlin



Photo credit:
Sandra Barton Vickers

ABSTRACT. In 2007, the US west coast shellfish industry began to feel the effects of unprecedented levels of larval mortality in commercial hatcheries producing the Pacific oyster *Crassostrea gigas*. Subsequently, researchers at Whiskey Creek Shellfish Hatchery, working with academic and government scientists, showed a high correlation between aragonite saturation state (Ω_{arag}) of inflowing seawater and survival of larval groups, clearly linking increased CO_2 to hatchery failures. This work led the Pacific Coast Shellfish Growers Association (PCSGA) to instrument shellfish hatcheries and coastal waters, establishing a monitoring network in collaboration with university researchers and the US Integrated Ocean Observing System. Analytical developments, such as the ability to monitor Ω_{arag} in real time, have greatly improved the industry's understanding of carbonate chemistry and its variability and informed the development of commercial-scale water treatment systems. These treatment systems have generally proven effective, resulting in billions of additional oyster larvae supplied to Pacific Northwest oyster growers. However, significant challenges remain, and a multifaceted approach, including selective breeding of oyster stocks, expansion of hatchery capacity, continued monitoring of coastal water chemistry, and improved understanding of biological responses will all be essential to the survival of the US west coast shellfish industry.

INTRODUCTION

The coastal ocean along the west coast of the United States supports some of the most productive fisheries in the world, including the 120-year-old Pacific Northwest shellfish industry. Seasonal coastal upwelling, which annually supplies nutrient-rich water to the inner continental shelf from late spring to early fall, drives this productivity. However, the same upwelling that fuels the industry also threatens it. Decomposition of organic matter at depth naturally raises CO_2 in upwelled seawater, and increasing atmospheric CO_2 concentrations have raised the baseline, leading to increased intensity, magnitude, and duration of acidified water over the continental shelf (Feely et al., 2008; Hauri et al., 2009, 2013; Gruber et al., 2012).

When gaseous CO_2 dissolves in seawater, it reacts with the water to form a weak acid (H_2CO_3), which dissociates to release a hydrogen ion ($\text{H}_2\text{CO}_3 \rightleftharpoons \text{H}^+ + \text{HCO}_3^-$) or reacts directly to consume carbonate ions ($\text{H}_2\text{CO}_3 + \text{CO}_3^{2-} \rightleftharpoons 2\text{HCO}_3^-$). This acidification process decreases the saturation state of aragonite (Ω_{arag}) and calcite (Ω_{cal}), the two mineral forms of calcium carbonate that most bivalves use to form their shells. A variety of shell-forming organisms have been shown to be highly

sensitive to the effects of ocean acidification (OA), such as reduced saturation state (Fabry et al., 2008; Hofmann et al., 2010; Hettinger et al., 2012; Bednaršek et al., 2012, 2014; Gazeau et al., 2013; Kroeker et al., 2010, 2013; Gaylord et al., 2014), including many commercially important shellfish species (Kurihara et al., 2007; Green et al., 2009; Miller et al., 2009; Talmage and Gobler, 2011; Barton et al., 2012; Hettinger et al., 2012; Waldbusser et al., 2013, 2015). Organisms that deposit calcareous shells or skeletons may respond to decreasing Ω_{arag} at values as high as 2, and are expected to encounter increasing physiological challenges as carbonate saturation decreases in the ocean (Fabry et al., 2008; Barton et al., 2012; Bednaršek et al., 2012, 2014; Waldbusser et al., 2015). Except for a few studies at underwater seeps that vent CO_2 , this research has almost exclusively been carried out in laboratories, where saturation states were reduced with CO_2 and held constant to match the expected changes in surface ocean chemistry several decades in the future.

Recent research shows a clear link between natural variability in seawater Ω_{arag} along the Oregon coast and commercial production of Pacific oyster larvae in a hatchery setting, where food and water temperatures are maintained

at optimal levels, but the chemistry of incoming seawater varies (Barton et al., 2012). Subsequent work, in part the result of monitoring larval oysters in shellfish hatcheries, documents a mechanism for direct Ω_{arag} sensitivity in early shell formation of bivalve larvae (Waldbusser et al., 2013; 2015), responses previously thought to be related solely to changes in the organisms' acid-base chemistry (Pörtner, 2008). These findings have immediate implications for the Pacific Northwest shellfish industry, which has experienced significant seed shortages since 2007.

In nearshore California Current surface waters off the coast of Oregon, the increase in atmospheric CO_2 has shifted the median Ω_{arag} from approximately 2.5 to 2.0 (Feely et al., 2008; Harris et al., 2013), and values of Ω_{arag} less than 2.0 are already common throughout the spring and summer across major sections of US Pacific coastal waters and Puget Sound (Feely et al., 2008, 2010, 2012b; Hauri et al., 2009). OA has contributed significantly to shoaling of Pacific Northwest aragonite and calcite saturation horizons (Feely et al., 2012b), and recent observations along the Oregon/Washington coast have recorded $\Omega_{\text{arag}} < 1.0$ in upwelled water at the surface, a condition not expected in the open ocean for decades (Feely et al., 2008). Modeling of the California Current System predicts that this trend will continue and accelerate relative to the open oligotrophic ocean, with undersaturated conditions in surface waters predicted to be the norm more than 50% of the time during summer by 2050 (Gruber et al., 2012; Hauri et al., 2011, 2013).

These changes in Pacific Northwest ocean conditions have already resulted in major oyster seed production declines (Barton et al., 2012; Washington State Blue Ribbon Panel on Ocean Acidification, 2012), and the shellfish industry has adopted a comprehensive strategy to understand, and mitigate, further impacts on commercial production (Washington State Blue Ribbon Panel on Ocean Acidification, 2012). Using funding from state, federal, and industry

groups, shellfish hatcheries have forged partnerships with university researchers, and are now some of the best instrumented monitoring stations for collecting carbonate chemistry measurements in the coastal zone. Industry uses these monitoring data as a real-time management tool to optimize water treatment systems and improve commercial production of oyster larvae. Additionally, hatcheries provide a perfect environment for monitoring biological responses, given that typical hatchery protocols require routine tracking and measurement of larval cohorts. The industry has capitalized on this by forging relationships with physiologists and geneticists to determine the mechanisms behind larval mortality events and develop long-term strategies to adapt to further declines in water quality predicted for the coming decades.

More importantly, the shellfish farming industry has become a catalyst for change. The partnerships industry members have developed with the scientific community helped shift the focus of OA research from oceanic to coastal environments, where there are many additional drivers and more complex natural temporal patterns (Hinga, 1992; Frankignoulle et al., 1998; Ringwood and Keppler, 2002; Wootton et al., 2008; Juranek et al., 2009; Hofmann et al., 2010; Alin et al., 2012; Harris et al., 2013; Feely et al., 2012a; Waldbusser and Salisbury, 2014). In addition, the shellfish industry's challenges helped refocus OA management away from solely pursuing global carbon reduction, and encouraged managers to pursue actions that can be taken locally to mitigate OA effects on coastal waters throughout the Pacific Northwest (Kelly et al., 2011; Washington State Blue Ribbon Panel on Ocean Acidification, 2012). In 2013, Washington became the first state to develop a comprehensive management strategy to protect its resources from OA effects, largely in response to concerns raised by the shellfish industry. This paper describes the factors that drew the shellfish industry into this issue; how the partnerships established among industry,

academia, federal and state scientists, and the local management community flourished in ways that benefited all sectors; and the industry's strategy to adapt as OA continues to advance globally.

PACIFIC NORTHWEST SHELLFISH INDUSTRY

Shellfish have been harvested in the Pacific Northwest for thousands of years, and commercial oyster farming has been an important cultural and economic part of coastal communities in the Northwest since the late 1800s. Today, shellfish farming supports over \$270 million in economic activity and over 3,000 family wage jobs in rural areas throughout the region. Although shellfish farms can be found throughout Oregon, Washington, Alaska, California, and Hawaii, most of the oysters harvested in the Pacific Northwest are produced in Washington. Large farms in Willapa Bay and southern Puget Sound make up the majority of the industry, and have existed in these areas for several generations (<http://pcsga.org/shellfish-initiative>).

Shellfish species farmed in the Pacific Northwest include Manila clams (*Venerupis philippinarum*), geoduck clams (*Panopea generosa*), mussels (*Mytilus trossulus* and *M. galloprovincialis*), and several species of oysters. Although Kumamoto oysters (*Crassostrea sikamea*), eastern oysters (*Crassostrea virginica*), and the native Olympia oyster (*Ostrea conchaphila*) represent important niche markets, the Pacific oyster (*Crassostrea gigas*) is the predominant species farmed in the region, comprising >80% of the industry's total annual shellfish production by live weight (Table 1).

Pacific oysters from Japan were first brought to the United States in the early twentieth century, and naturalized populations became established in portions of Puget Sound and in Willapa Bay. Natural recruitment of seed oysters from these spawning populations helped support the industry for several decades, supplementing the supply of imported seed from Japan. In the 1970s, the cost of importing

seed became prohibitively expensive, and it became clear that growers could not rely solely on inconsistent natural spawning events (Dumbauld et al., 2011) to support their burgeoning industry (Gordon and Blanton, 2001).

By the late 1970s, successful commercial hatcheries were established in the Pacific Northwest and began supplying billions of "eyed" (setting size) larvae to growers each year. The three major commercial hatcheries that currently supply larvae to the West Coast shellfish industry are Whiskey Creek Shellfish Hatchery (Netarts Bay, OR), Taylor Shellfish Hatchery (Dabob Bay, WA), and Coast Seafoods Hatchery (Quilcene Bay, WA). These hatcheries combine with smaller hatcheries in Washington and Hawaii to produce 40–60 billion eyed larvae each year, and their 30 years of consistent production has helped build today's \$270 million per year shellfish industry (<http://pcsga.org/shellfish-initiative>).

Hatchery Failures

High levels of larval mortality at the Whiskey Creek Shellfish Hatchery began in July 2007 and persisted to the end of the growing season in October. Some month-to-month variability in hatchery production is normal, but the magnitude and duration of the 2007 mortality events were unprecedented in the hatchery's 30-year history. Hatchery managers initially attributed the mortality to a large bloom of *Vibrio tubiashii* in Netarts Bay, a bacterium pathogenic to oyster larvae (Elston et al., 2008). However, larval mortality persisted even after successful elimination of the pathogen, forcing managers to search for another explanation for the die-offs.

By early summer of 2008, hatchery personnel shifted their focus away from biological pathogens and for the first time began investigating seawater chemistry as a potential explanation for the persistent summertime mortality events. A large mortality event in July 2008 triggered these investigations, which coincided with a large upwelling event along

the Washington-Oregon coast. This strong upwelling event brought seawater undersaturated with respect to aragonite to the surface and across the continental shelf into Netarts Bay, and hatchery managers recorded pH values as low as 7.6 near hatchery intakes. Preliminary experiments conducted in July and August 2008 showed a marked improvement in the survival and growth of larval cohorts when pH was adjusted by adding sodium carbonate, providing the first clear evidence that carbonate chemistry had affected hatchery production.

These findings came too late in the 2008 production season to be of immediate commercial benefit, however, and overall production at Whiskey Creek in 2008 was approximately 2.5 billion eyed larvae, about 25% of a normal season's production. Whiskey Creek is the primary supplier of larvae to many independent growers throughout the Pacific Northwest, and the shortage of larvae from the hatchery, combined with several consecutive years of poor natural recruitment of larvae from spawning populations in Willapa Bay (Dumbauld et al., 2011), generated concern among

growers across the entire West Coast shellfish industry.

The annual growers meeting held in September 2008 represented an important turning point for the industry, when the keynote speaker, Richard Feely, introduced oyster growers to the potential impacts of OA on shellfish. Combined with preliminary indications from Whiskey Creek that acidified seawater played a major role in the hatchery's production problems that summer, the meeting served as a call to action for the entire industry, and provided an initial forum for researchers, hatchery managers, and growers to discuss the problem face-to-face and propose a strategy to better understand OA's impacts on the industry.

INSTRUMENTING THE HATCHERIES

First Attempts at Monitoring (2009)

In spring 2009, Whiskey Creek Shellfish Hatchery initiated a comprehensive water quality monitoring program, funded by the Pacific Coast Shellfish Growers Association (PCSGA) and the Willapa Bay Reserve Fund. This initial

monitoring included continuous measurement of pH, dissolved oxygen, temperature, salinity, and pressure, as well as weekly discrete samples for bacteria, nutrient concentrations, and total carbonate chemistry. Carbonate chemistry samples were sent for analysis to the laboratory of author Hales at Oregon State University (<http://ceoas.oregonstate.edu/profile/hales>), establishing an important connection between the shellfish industry and the chemical oceanographic community.

Data collected throughout summer 2009 were then correlated against production metrics routinely recorded at the hatchery, and the results showed a clear link between Ω_{arag} and the survival and growth of larval cohorts in the hatchery. In particular, these data showed that Ω_{arag} during first-shell development (the first 24–48 hours after fertilization of eggs) was critical to the ultimate survival and growth of larval groups (Figure 1), and $\Omega_{\text{arag}} > 1.7$ represented the “break-even” point for commercial production at Whiskey Creek (Barton et al., 2012). These findings offered the first clear evidence of OA impacts on larval

TABLE 1. US West Coast shellfish production estimates for 2009 (the most recent data available) compiled by the Pacific Coast Shellfish Growers Association (PCSGA). Shellfish sales are divided by species and by state, and when available, total sales are shown both by live weight and economic value. Data for this table were compiled by Ted Kuiper and Jim Gibbons.

		Oysters Current*	Clams Current*	Mussels Current*	Geoduck Current*	All Shellfish Larvae and Seed	Total Current
Washington	Pounds	61,000,000	9,520,000	2,750,000	1,650,000		74,920,000
	Sales	\$57,750,000	\$19,550,000	\$3,162,500	\$20,100,00	\$7,000,000	\$107,562,500
California	Pounds	9,270,995	741,463	315,000			10,327,458
	Sales	\$12,361,326	\$830,000	\$945,000		\$2,300,000	\$16,436,326
Oregon	Pounds	2,379,988					2,379,988
	Sales	\$2,253,135				\$750,000	\$3,003,135
Alaska	Pounds	206,709	7,839	1,988			216,536
	Sales	\$441,781	\$24,841	\$6,610		\$126,000	\$599,232
Total	Pounds	72,857,692	10,269,302	3,066,988	1,650,000		87,843,982
	Sales	\$72,806,242	\$20,404,841	\$4,114,110	\$20,100,000		\$117,425,193

*All pounds converted to live weight/in the shell

Compiled by the Pacific Coast Shellfish Growers Association. All production data represent most recent info available from:

Alaska Dept of Fish and Game (2009)

Oregon Dept of Agriculture (2009)

Powell, Seiler and Co, Certified Public Accountants for Willapa (2008)

Shellfish companies in California (2008) and Washington (2008, 2009)

organisms in the natural environment under naturally fluctuating conditions that have been magnified by increasing atmospheric CO₂ (Barton et al., 2012; Waldbusser et al., 2013).

Subsequent research confirmed that Ω_{arag} values significantly >1.0 are required to support proper development of Pacific oyster larvae (Barton et al., 2012; Waldbusser et al., 2013, 2015). Pacific oyster larvae develop from an egg (0% shell) to D-hinge oyster larvae (~80% shell) in a period of less than 24 hours (and it appears to be closer to a six-hour window; Waldbusser et al., 2015), representing a tremendous energetic bottleneck due to the rapid rate of calcification (Waldbusser et al., 2013). During this rapid shell development, analysis of stable C isotopes indicates that the shell is precipitated in greater contact with surrounding water, increasing susceptibility to ambient water saturation state (Waldbusser et al., 2013; Figure 2). Recent experiments show that Ω_{arag} , not pH or $p\text{CO}_2$, is the primary variable impacting larval development and growth during these early stages (Waldbusser et al., 2015).

Knowing that the first two days of development are critical to the survival of larval groups, managers timed their

spawning to coincide with afternoon photosynthetic activity, which raised saturation states outside the hatchery. Although not a perfect strategy, managers saw immediate improvements in the survival and growth of larval cohorts, and using real-time monitoring to “pick their moments” allowed Whiskey Creek to significantly improve summertime larval production in 2009 and 2010. In 2011, large-scale buffering systems were installed in Whiskey Creek Hatchery, and in 2012, hatcheries shifted production cycles earlier in the year to increase seed production before upwelling begins.

Development of the Pacific Coastal Shellfish Growers Association Monitoring Program

Whiskey Creek’s initial success with water quality monitoring in 2009 produced two important findings for the entire shellfish industry: (1) understanding, and adapting to, water chemistry in commercial hatcheries is extremely

important to seed production and, ultimately, to the economic resiliency of the Pacific Northwest shellfish industry; and (2) simple pH measurements are inadequate for developing a full understanding of the impacts of shifting carbonate chemistry on larvae, and measurement of Ω_{arag} is necessary for determining the impact of water chemistry on the initial development and ultimate survival of oyster larvae (Waldbusser et al., 2013, 2015).

In the winter of 2009–2010, PCSGA growers submitted a proposal to Senator Maria Cantwell’s (WA) office, requesting funds to build a monitoring network in areas of commercial importance to the industry. This proposal stressed the immediacy of the industry’s seed supply problems, and the potential for high-resolution, real-time data to improve seed supply for the entire industry. With Senator Cantwell’s support, National Oceanic and Atmospheric Administration (NOAA) funds were allocated in early 2010, and PCSGA monitoring stations were quickly

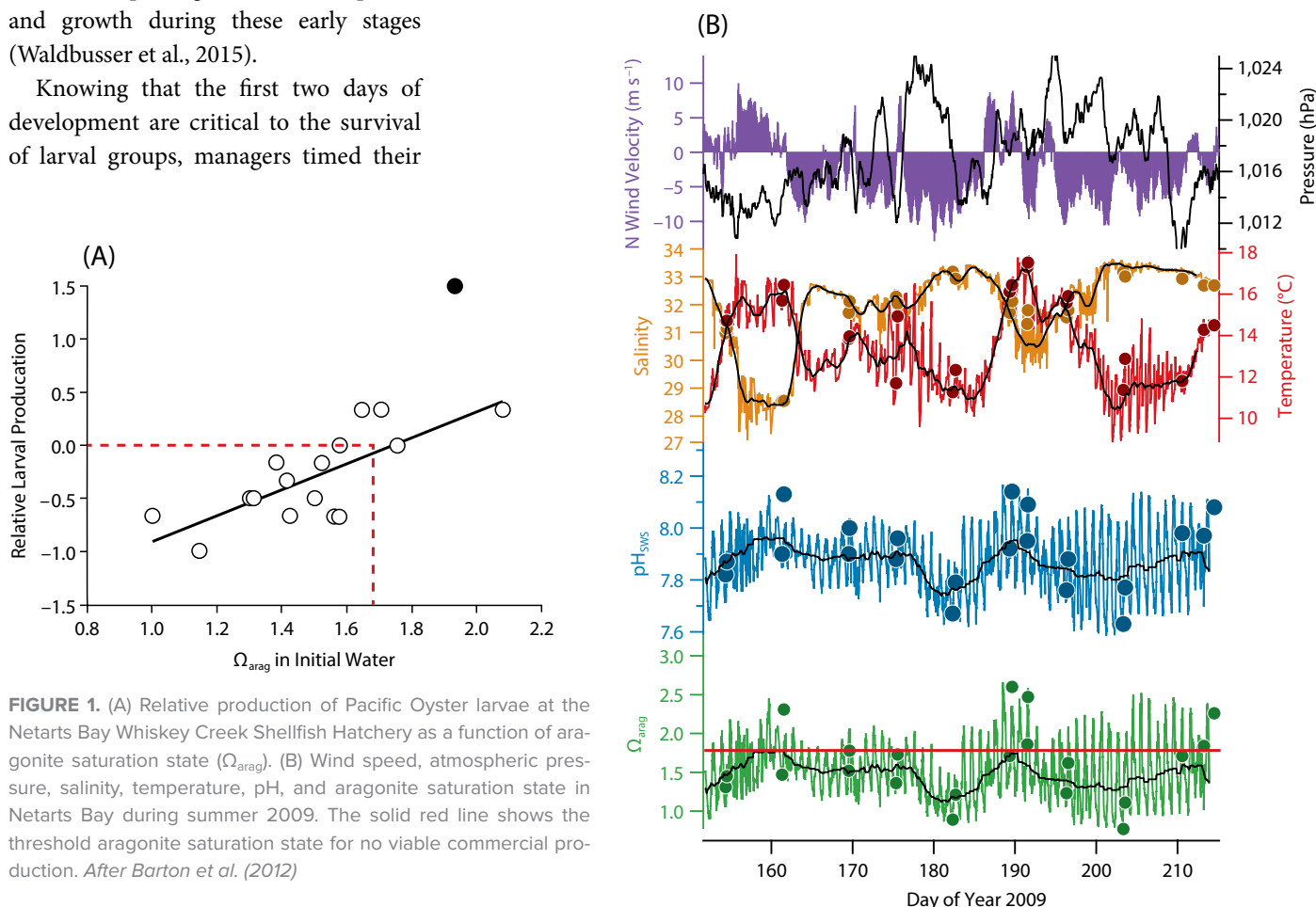


FIGURE 1. (A) Relative production of Pacific Oyster larvae at the Netarts Bay Whiskey Creek Shellfish Hatchery as a function of aragonite saturation state (Ω_{arag}). (B) Wind speed, atmospheric pressure, salinity, temperature, pH, and aragonite saturation state in Netarts Bay during summer 2009. The solid red line shows the threshold aragonite saturation state for no viable commercial production. After Barton et al. (2012)

established to characterize water chemistry at Whiskey Creek Shellfish Hatchery, Taylor Shellfish Hatchery, the Lummi Nation Shellfish Hatchery, and at three sites in Willapa Bay (Tokeland, Bay Center, and Nahcotta) (Figure 3; Table 2). These funds allowed PCSGA to expand the model originally adopted at Whiskey Creek, and continuous data (pH, temperature, salinity, and dissolved oxygen) from the monitoring sites were combined with routine discrete sampling for bacteria, nutrient concentrations, and total carbonate chemistry. The award also supported construction of three continuous (1 Hz) $p\text{CO}_2$ monitoring systems that were designed and constructed at Oregon State University (<http://ceoas.oregonstate.edu/profile/hales>). The first of these

systems was installed at Whiskey Creek in April 2010, and by spring 2011, sensors were operational at Taylor Shellfish Hatchery and in Willapa Bay, with supplementary funding from the Educational Foundation of America (EFA).

The ability to observe carbonate chemistry data in real time has fundamentally altered the way shellfish hatchery managers view seawater chemistry in the Pacific Northwest. The data streams generated at commercial hatcheries and distributed through the US Integrated Ocean Observing System (IOOS) regional Northwest Association of Networked Ocean Observing Systems (NANOOS) data portal serve as an important management tool for growers throughout the industry. For both Whiskey Creek

and Taylor Shellfish hatcheries (and for growers utilizing monitoring data to improve commercial sets), the PCSGA Monitoring Program put the proverbial “headlights on the car.” Access to real-time carbonate chemistry data provides a clear connection between OA and larval mortality as well as an explanation for the recent decline in commercial larval production.

Turning on the High Beams: Interactions with C-CAN, the Burke-O-Lator 3000, and New IOOS Sensor Development

Although real-time measurement of $p\text{CO}_2$ provided essential data to commercial hatchery managers, $p\text{CO}_2$ is, like pH, a proxy for seawater Ω_{arag} , the parameter

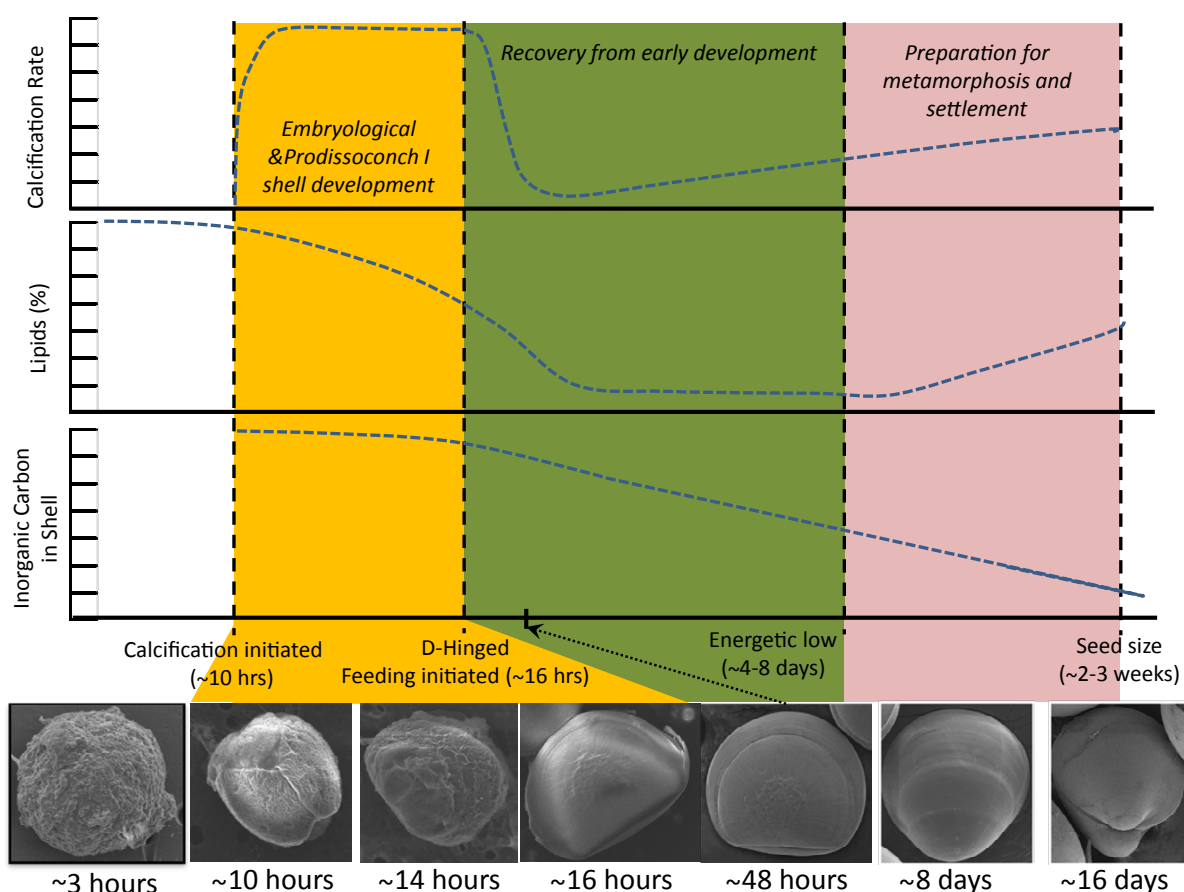


FIGURE 2. Trends in relative biochemistry and shell morphology in Pacific oyster larvae raised in the Whiskey Creek Shellfish Hatchery. Bottom axis is time on a nonlinear scale, relating to stages of larval ontology from hours after fertilization to settlement two to three weeks later. Shell diameters in scanning electron microscope images increase from ~75 μm to ~320 μm at settlement size. Panels for calcification rate, % lipids, and inorganic carbon in shell are in relative scales to highlight the changes occurring in the early shell development stage (yellow), when the primary energy source is maternally derived lipids. During this initial period, there is high incorporation of seawater inorganic carbon and high sensitivity to saturation state effects. Even if larvae manage to develop under moderate saturation state stress, they are smaller at the completion of this period (Waldbusser et al., 2015), and fewer proceed to metamorphosis (Barton et al., 2012).

most closely associated with initial shell formation and survival of oyster larvae (Waldbusser et al., 2015). Gaining a true understanding of carbonate chemistry variability and its effects on shellfish larvae therefore required another technological leap forward for both the shellfish industry and the chemical oceanographic community.

A workshop held in Costa Mesa, CA, in July 2010 facilitated this next step, and concern from shellfish growers and wild harvest fisherman alike helped bring together a diverse group of scientists, shellfish industry representatives, commercial fishermen, and resource managers from local, state, federal, and tribal groups (Southern California Coastal Water Research Project, 2010). These parties recognized the threat OA poses

to valuable commercial fisheries across the Pacific Northwest and the need for a coordinated regional approach to the problem. The workshop led to a partnership among these groups and recognition that coastal zone acidification represents new scientific and management challenges compared to acidification studies in the open ocean. Until then, limited work on OA had been conducted in nearshore environments (e.g., Ringwood and Keppler, 2002; Green et al., 2009), with most oceanographic research focused on decadal-scale changes in the open ocean (Feely et al., 2008, 2012b). The workshop illustrated that coastal effects operate around tidal, diurnal, and seasonal patterns that were not well understood, requiring additional monitoring and analysis.

This workshop ultimately resulted in formation of the California Current Acidification Network (C-CAN), a unique partnership dedicated to: (1) encouraging development of an OA monitoring network for the West Coast, (2) understanding the linkages between oceanographic conditions and biological responses, (3) encouraging development of causal, predictive, and economic models that characterize these linkages and forecast effects, and (4) facilitating communication and resource/data sharing among the many organizations that participate in C-CAN in collaboration with US IOOS (<http://c-can.msi.ucsb.edu>).

In subsequent workshops, C-CAN helped define the parameters most important to monitor in coastal systems and developed a detailed set of Core Monitoring Principles (McLaughlin et al., 2015, in this issue) to help industry representatives obtain research quality data from their monitoring systems. A major outcome of these workshops was definition of a benchmark that requires Ω_{arag} to be measured within ± 0.2 in order to be biologically relevant, based on variance often seen in experimental studies of species responses. Although this level of accuracy is generally attainable in open-ocean systems, the complexities of dynamic coastal estuaries make it a more challenging task in these environments (Feely et al., 2010; Harris et al., 2013). C-CAN's Core Monitoring Principles provide specific direction to assist industry personnel in optimizing data quality, including recommendations on available instrumentation, protocols for proper calibration of equipment, and recommendations for routine Quality Assurance/Quality Control with outside laboratories.

Additionally, C-CAN provided a forum for face-to-face interactions between industry personnel and researchers and extended these interactions beyond the hatcheries to a wider audience of shellfish growers and commercial fishermen. These conversations allowed growers throughout the industry to obtain a basic

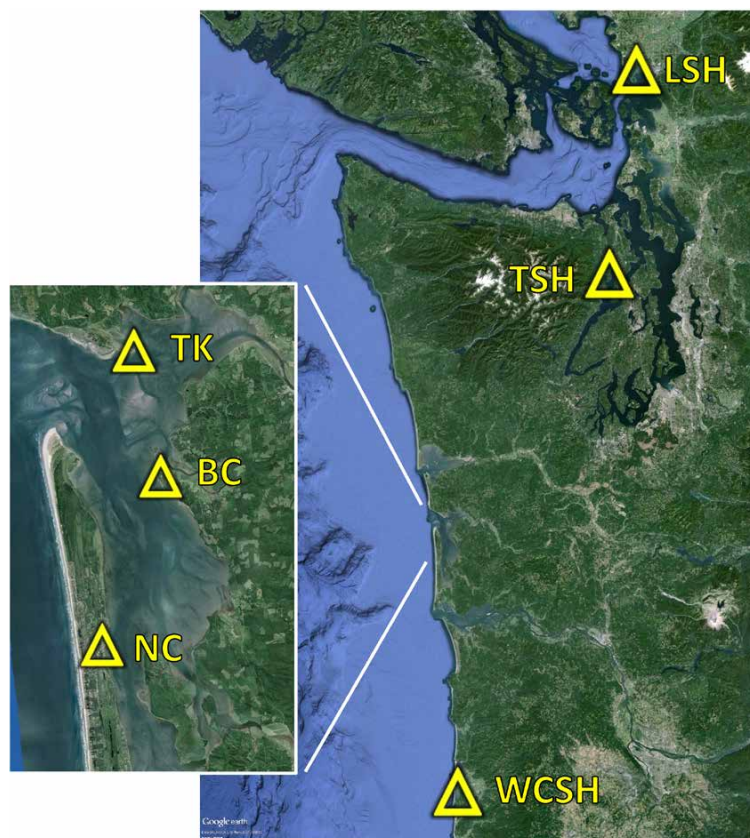


FIGURE 3. Monitoring sites established in 2011 by the Pacific Coast Shellfish Growers Association (PCSGA). Main map: LSH = Lummi Shellfish Hatchery, Bellingham, WA. TSH = Taylor Shellfish Hatchery, Dabob Bay, WA. WCSH = Whiskey Creek Shellfish Hatchery, Netarts Bay, OR. Inset of Willapa Bay: TK = Tokeland. BC = Bay Center (Ekone Oyster Co.). NC = Nahcotta (Jolly Roger Oyster Co.). Three new sites were added in 2014, in Alaska and California, as partnerships between shellfish growers and NOAA, and additional sites are planned.

TABLE 2. Summary of monitoring sites of the Pacific Coast Shellfish Growers Association, insights gained from monitoring, and associated mitigation strategies.

Site	Location	Site Characteristics	Insights Gained from Monitoring	Mitigation Strategies
Whiskey Creek Shellfish Hatchery	Netarts Bay, OR	Whiskey Creek is a shallow (<10 m deep), largely oceanic bay with little freshwater input Strongly influenced by offshore conditions including direct intrusions of high salinity (>33 ppt) upwelled water during summertime	Identified large-scale shifts in seawater chemistry associated with the intrusion/relaxation of upwelled seawater into Netarts Bay (2009)	Buffered tanks using sodium carbonate Increased frequency of spawning immediately after strong north winds began (because 24–48 hours of sustained north winds are required to advect upwelled water across the Oregon continental shelf and into Netarts Bay) to create large groups of larvae prior to intrusion of upwelled water into Netarts Bay
			Revealed large diel pH/O ₂ variability associated with photosynthetic activity of eelgrass and algae in the bay (2009) and the estuary's dynamic responses to these forcings	"Picked their moments" to utilize afternoon (high pH, high O ₂) water for spawning
			Provided hatchery with an understanding of how carbonate chemistry and oxygen levels evolve in the bay throughout the growing season. Conditions deteriorate in late summer/fall due to prolonged periods of upwelling and associated decomposition of high volumes of organic matter, both within Netarts Bay (eelgrass, etc.) and offshore over the Oregon continental shelf	Shifted production season earlier each year to place less reliance on late season (August–October) production Refined treatment systems to oxidize incoming seawater. Additional work is required to address late season conditions at the hatchery
Taylor Shellfish Hatchery	Dabob Bay, WA	Dabob Bay is a deep (>100 m) bay off Hood Canal Strongly influenced by local processes within Hood Canal due to long residence times once offshore water intrudes into the canal over a shallow (~25 m) sill at Admiralty Inlet	Monitoring revealed a marked difference in pCO ₂ concentrations from shallow (5–15 m) and deep (100 m) water intakes at the hatchery. Deep water has persistently high pCO ₂ (generally >800 µatm)	Provided an explanation for poor survival commonly observed when deep water was used for rearing oyster larvae (Figure 4)
			Monitoring revealed that periodic, wind-driven mixing of the entire water column in Dabob Bay leads to a significant increase in the pCO ₂ water of surface waters outside the hatchery, with potential negative impacts on larval production	Developed treatment systems similar to those at Whiskey Creek to buffer and improve oxidation state of incoming seawater
Bay Center Nahcotta Tokeland	Willapa Bay, WA	Willapa Bay is a large coastal bay with long residence times in the southern portion of the bay (Banas et al., 2007) and significant freshwater input from coastal rivers, which may complicate or overwhelm the signal from an offshore upwelling event Unlike hatcheries, larvae in the natural environment face wide variations in temperature, salinity, and food availability, and any of these factors may play important roles in determining the success or failure of a larval cohort (Ruesink et al., 2003)	Monitoring has shown that Ω_{arag} during the summer often falls well below the optimal threshold (of $\Omega_{\text{arag}} > 1.7$) for larval development As OA advances in coming decades, the window of opportunity for spawning events to coincide with favorable water chemistry will continue to shrink (Rykaczewski and Dunne, 2010; Gruber et al., 2012; Hauri et al., 2011, 2013; recent work of author Hales and colleagues), adding a significant stressor to the list of factors impacting the survival of shellfish larvae in natural systems	Growers use real-time data from NANOOS to time filling of setting tanks Some farms are now buffering setting tanks with carbonate After seven to eight years of sub-par commercial sets (recruitment of naturally occurring larvae to shell bags placed in the bay (Dumbauld et al., 2011), many growers who relied on natural spawning events to seed their farms for decades have instead begun purchasing shell bags seeded with hatchery larvae, increasing overall demand for larvae
Lummi Hatchery	Bellingham, WA	The Lummi hatchery draws seawater from a large (700 acre) sea pond off Puget Sound	Monitoring has revealed significant differences between pond water and waters of the outer sound, where conditions are more variable	The pond may act as a buffer/refuge against extreme events in the surrounding ocean

understanding of how carbonate chemistry is measured and how those measurements can be used to calculate Ω_{arag} , the quantity of interest to shellfish farmers. These discussions helped greatly in refining the direction of PCSGA's monitoring effort, and can be summarized as follows:

Ω_{arag} can be calculated from any two of four measurable parameters in the carbonate system (pH, $p\text{CO}_2$, total alkalinity, and dissolved inorganic carbon [DIC]), if they are measured within a required level of precision and accuracy, and if accurate temperature and salinity measurements are

recorded simultaneously. Although pH sensors are readily available, many are unable to achieve the level of precision required to calculate Ω_{arag} within ± 0.2 ; selection of appropriate pH sensors, along with proper calibration, is therefore essential if they are to be used in calculating Ω_{arag} . Instruments to measure $p\text{CO}_2$ are costly, but are commercially available, making pH and $p\text{CO}_2$ an obvious pair of parameters for shellfish growers to use in calculating Ω_{arag} . However, pH and $p\text{CO}_2$ covary and can both be highly dynamic in coastal systems, introducing error into the calculation of Ω_{arag} . Therefore, it is preferable to use one of these quantities, paired with either DIC or total alkalinity (both of which are less variable in coastal environments), to have the best chance of reliably measuring Ω_{arag} in coastal bays and estuaries.

Following C-CAN advice, PCSGA monitoring stations upgraded their pH sensor technology after the 2010 workshop. Combined with the $p\text{CO}_2$ sensors installed at Whiskey Creek, Taylor Shellfish Hatchery, and in Willapa Bay, growers were for the first time able to generate real-time Ω_{arag} estimates, albeit from measurements of pH and $p\text{CO}_2$ only (or through use of emerging relationships between total alkalinity and salinity).

At the same time, the shellfish industry began working toward measuring DIC and $p\text{CO}_2$ in near-real time to obtain the best possible measurement of Ω_{arag} . Using funds provided under the NOAA/Cantwell award, Oregon State University oceanographers modified the existing $p\text{CO}_2$ monitoring system at Whiskey Creek into a combined $p\text{CO}_2/\text{tCO}_2$ system, and by the end of 2013, the Burke-O-Lator 3000 emerged as a robust sensor for real time calculation of Ω_{arag} , capable of meeting the C-CAN precision standard of ± 0.2 for extended periods of continuous use. The robustness of this system stems largely from recognizing that sensors will ultimately fail in dynamic coastal environments. Therefore, rather than relying solely on measurement of $p\text{CO}_2$ and DIC to calculate Ω_{arag} , the

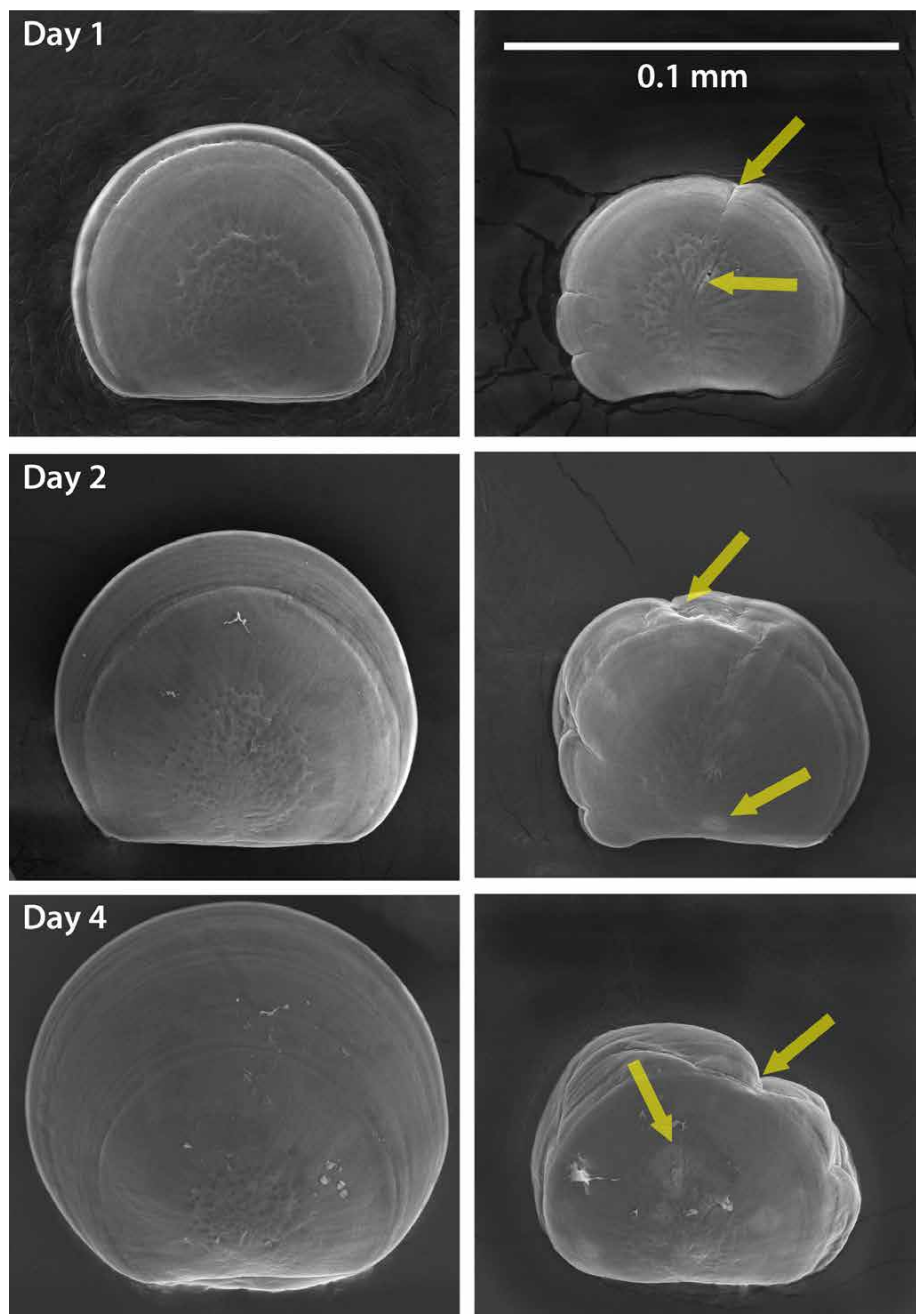


FIGURE 4. Pacific oyster larvae from the same spawn, raised by the Taylor Shellfish Hatchery in natural waters of Dabob Bay, WA, exhibiting favorable (shallow intake, left column, $p\text{CO}_2 = 403$ ppm, $\Omega_{\text{arag}} = 1.64$, and $\text{pH}_T = 8.00$) and unfavorable (deep intake, right column, $p\text{CO}_2 = 1418$ ppm, $\Omega_{\text{arag}} = 0.47$, and $\text{pH}_T = 7.49$) carbonate chemistry during the spawning period. Scanning Electron Microscopy (SEM) images show representative larval shells from each condition at one, two, and four days post-fertilization. Under more acidified conditions, shell development is impaired; arrows show defects (creases) and features (light patches on shell) suggestive of dissolution.

Whiskey Creek system also measures pH using a Durafet III sensor, ensuring that three of the four parameters in the carbonate system are measured continuously. In addition, five years of routine data collection at Whiskey Creek have provided sufficient data for oceanographers to define the local relationship between total alkalinity and salinity, allowing salinity to be used as a proxy measurement for alkalinity. Thus, the carbonate system can be fully constrained at Whiskey Creek.

This oversampling allows for calculation of Ω_{arag} from several different pairs of carbonate system measurements, which can be compared against one another. Currently, the Whiskey Creek system is capable of calculating, and displaying in real time, five calculated values for Ω_{arag} (from pH/DIC, $p\text{CO}_2$ /DIC, $p\text{CO}_2$ /TA, DIC/TA, pH/ $p\text{CO}_2$). By adding the capability for remote access to the system, the Hales laboratory can view data, make adjustments as needed, and quickly identify the need for system maintenance if any discrepancies arise between the independent calculations of Ω_{arag} .

This capability is key to the success of any monitoring partnership between shellfish growers and oceanographers. Most growers lack the familiarity with carbonate chemistry to identify errors in a time series quickly, and budgetary constraints limit the amount of time that researchers can spend traveling to and from commercial hatcheries. Remote access to the data allows researchers to identify sensor failures quickly and deploy technicians as needed to optimize the overall quality of the time series.

A newly awarded grant from US IOOS and the NOAA OA Program's "Ocean Technology Transition" competition will allow the Hales laboratory to develop new lower cost and higher accuracy $p\text{CO}_2$ sensor technology for OA monitoring, with expansion to new sites as advised by PCSGA. It will also strengthen existing regional partnerships through IOOS regional associations along the Pacific coast to implement and provide quality-assured tests of the new sensors.

Dubbed "turning the headlights on high," this project seeks to improve and institutionalize the partnerships and successes to date, while commercializing a more stable and less costly $p\text{CO}_2$ sensor desired by shellfish growers.

EXPANDING THE PARTNERSHIP WITH OA SCIENTISTS

The PCSGA Monitoring Program's insistence on a high level of precision has had an immediate synergistic effect. When researchers developed the capability to actively monitor time series and maximize the overall quality of the data stream, the monitoring program became not only a sophisticated tool for helping shellfish hatcheries but also a resource for high quality, publishable carbonate chemistry data from coastal locations previously undocumented in efforts to monitor the coastal ocean.

These data are particularly valuable for quantifying the impacts of OA on coastal estuaries throughout the Pacific Northwest because the chemical monitoring stations were co-located with biological monitoring systems (i.e., hatchery production records; Table 2). This co-location allowed researchers to develop a better understanding of the response of biota to the chemical parameters and at what thresholds. Moreover, the continuous chemistry data helped refine laboratory-based acidification exposure studies. Whereas most physiological experiments prior to that time focused on changes in steady-state conditions, as might occur in the open ocean, the new temporally intensive data provided information on episodic exposures relating to the diurnal and tidal changes encountered by biota in nearshore habitats.

As an example, the work conducted at Whiskey Creek by researchers from Oregon State University has greatly increased scientific understanding of early shell formation in Pacific oyster larvae (Waldbusser et al., 2013), in addition to providing valuable insights to hatchery managers (Figures 2 and 3). Importantly, the larvae used in these studies were not

exposed to artificially acidified conditions in laboratory trials but rather showed OA impacts when grown in seawater drawn directly from Netarts Bay (Barton et al., 2012). Such collaborative work illustrates the role that the PCSGA Monitoring Program can play in engaging researchers to work in important shellfish growing areas and the mutual benefits to all parties as they attempt to understand, and adapt to, coastal acidification in the Pacific Northwest.

Similar partnerships have developed between researchers and shellfish growers throughout Washington State. The relocation of a NOAA buoy within Dabob Bay to waters adjacent to Taylor Shellfish Hatchery represents an example of the responsiveness of NOAA and University of Washington researchers to the needs of shellfish growers and the mutual benefits of comparing buoy data to instrumentation at the hatchery. These industry/research partnerships have spawned research in additional shellfish growing areas important to the industry (<http://www.pacshell.org/about-us.asp>; <http://www.ocean.washington.edu/home/Simone+Alin>), and helped identify potential sites for future expansion of the monitoring network.

Making Data Available to the Larger Community Through Interactions with NANOOS

Early on in the development of the PCSGA Monitoring Program, the shellfish industry began to interact with IOOS, and in particular with NANOOS, the regional IOOS authority responsible for the Pacific Northwest. NANOOS recognized the potential value of PCSGA's program in monitoring coastal locations not previously represented in the larger effort to monitor ocean conditions in the Pacific Northwest, and became an essential partner in the effort to display these data streams online.

The shellfish industry is very interested in sharing data online so that it is accessible to as many growers as possible. In areas like Willapa Bay, coastal

monitoring has become a valuable tool for growers with commercial setting stations because it helps them maximize the quality of water used to fill setting tanks. This can have dramatic impact on setting success and seed survival, and ultimately, the “bottom line” for shellfish growers. The partnership with NANOOS makes these data widely available to growers throughout the Northwest, as well as to the scientists involved.

Based on the success of the PCSGA Monitoring Program, the NOAA Ocean Acidification Program (OAP) subsequently worked with IOOS to provide three new $p\text{CO}_2$ /DIC combined systems, which were recently installed in California and Alaska. These instruments significantly increase the number of shellfish growing areas represented in coastal monitoring programs and greatly extend the geographic extent of near-shore carbonate chemistry monitoring in the Pacific Northwest. These data should enhance understanding of OA impacts on coastal estuaries throughout the region.

In 2013, a Blue Ribbon panel of experts in Washington State recommended that the state provide funding to continue the PCSGA Monitoring Program and provided a detailed set of recommendations to combat OA at the state level (Washington State Blue Ribbon Panel on Ocean Acidification, 2012). The resulting funding, along with an Oregon legislature award to support monitoring at Whiskey Creek, ensures that the monitoring network will continue to provide essential information to the shellfish industry. This funding also supported an upgrade of the existing $p\text{CO}_2$ monitoring system at Taylor Shellfish to a system capable of measuring $p\text{CO}_2$ and DIC. The improvement in data quality should facilitate better collaboration, as both hatcheries attempt to understand, and mitigate, OA effects on commercial production. The new IOOS-OAP award, leveraged with support from Washington and Oregon state funds, should extend the monitoring effort at least several years into the future.

DEVELOPMENT OF COMMERCIAL-SCALE TREATMENT SYSTEMS IN HATCHERIES

Research at Whiskey Creek Shellfish Hatchery has identified $\Omega_{\text{arag}} > 1.7$ as the minimum threshold for development of commercially viable larvae groups (Barton et al., 2012), although higher saturation states are preferred by hatchery managers. Monitoring at Whiskey Creek has shown that Ω_{arag} now rarely exceeds this minimum threshold throughout the growing season, although nearshore California Current waters were likely at least 0.5 units higher prior to large-scale CO_2 emissions from fossil fuels (Harris et al., 2013). Even in the spring, before the summertime upwelling season, Ω_{arag} is less than optimal, and the hatchery has responded by installing chemical buffering systems that modify Ω_{arag} in the hatchery year-round. These systems have been quite effective, restoring 30–50% of productivity lost in previous seasons and resulting in billions of additional eyed larvae supplied to growers each year. Discovering the link between acidification and seed production, and installation of buffering systems to correct the problem, has kept the hatchery in business, maintaining seed supply to dozens of growers in Oregon, Washington, and California.

Commercial treatment system development at Whiskey Creek has benefited greatly from close collaboration with Chris Langdon and the Molluscan Broodstock Program (MBP) at Oregon State University's Hatfield Marine Science Center in Newport, OR (<http://fw.oregonstate.edu/content/chris-langdon>). MBP has been an industry partner since its inception in 1996, developing high-yield Pacific oyster stocks for industry use. To produce these stocks, MBP operates a small research hatchery in Yaquina Bay, where production failures began as early as 2005, prior to the major production failures first observed at Whiskey Creek in 2007. Since 2007, MBP has worked

collaboratively with Whiskey Creek, and ongoing research at MBP continues to inform treatment system development at both Whiskey Creek and Taylor Shellfish hatcheries.

Although buffering systems have greatly improved production at Whiskey Creek, they are insufficient to completely repair water chemistry issues impacting commercial hatcheries. Just as OA affects larvae in the hatchery setting, it also has a potential impact on biology in coastal waters throughout the Pacific Northwest (Bednaršek et al., 2014). The link between persistent summertime upwelling and low oxygen/high carbon dioxide regions over the inner continental shelf has been well documented (Hales et al., 2005, 2006; Chan et al., 2008; Feely et al., 2008). These oceanic waters are advected into the many small estuaries along the Pacific Northwest coast and can result in decreased estuarine oxygen conditions (Brown and Power, 2011). In Netarts Bay, local natural processes add to the oceanic signal, and as large amounts of seagrass and benthic micro- and macro-algae generated through the summer season begin to decay in August–October each year, carbon dioxide is increased and oxygen decreased. Although there was no regular water chemistry monitoring in Netarts Bay prior to 2009, conditions at the hatchery were historically conducive to larvae growth in September and early October. Since 2007, however, September and October have been characterized by poor water quality in the bay, forcing an early end to the growing season.

Treatment systems designed to combat these secondary effects of OA have met with some limited success and are undergoing further development both at Whiskey Creek and at Taylor Shellfish Hatchery. However, shellfish growers throughout the Pacific Northwest have much more work ahead to first understand, and then correct, the late season deterioration of water conditions in coastal bays.

LONGER-TERM STRATEGIES TO COMBAT THE IMPACTS OF COASTAL OA ON THE INDUSTRY

Selective Breeding for OA Tolerance

One strategy to combat the advancement of OA in the Pacific Northwest involves the use of selective breeding to develop resistant stocks. Selective breeding of Pacific oysters in the Northwest began in 1996 with creation of the MBP. Selected broodstock, from both MBP and industry-based breeding programs, is now commonly used in commercial hatcheries. Although these existing stocks were not specifically selected for OA resistance, they have been reared in the coastal waters of the Pacific Northwest for four to five generations and may have developed some natural resistance to acidification stress. At Whiskey Creek Shellfish Hatchery, managers have elected to use only MBP-selected broodstock, based on anecdotal evidence that these stocks perform better even in early larval stages. Ongoing research, supported by both the Oregon and Washington legislatures, is specifically focused on selecting stocks that perform well when exposed to reduced saturation state, with particular emphasis on exposing oysters to low Ω_{arag} in early larval stages. These breeding efforts are unlikely to identify larvae that are totally resistant to OA, but the existing gene pool may produce larvae with some tolerance, representing another valuable tool for hatcheries to employ in combating acidification impacts on commercial larval production.

Expansion of Hatchery Capacity in Locations Outside the Pacific Northwest

Another strategy adopted by the shellfish industry to deal with OA in the Pacific Northwest involves expansion of existing hatchery facilities and construction of new facilities in remote locations. In particular, hatchery operations in Hawaii have expanded dramatically in the past three to four years, with the hope that these sites will be less impacted by OA

than sites in the Pacific Northwest. OA is a global problem, however, so these efforts at best represent a short-term solution to carry the industry forward for the next few decades. Shellfish growers are aware of this fact, and the sheer amount of capital investment going into these adaptation strategies speaks volumes about the level of concern felt among growers throughout the Northwest.

EMERGENCE OF THE SHELLFISH INDUSTRY AS A SPOKESGROUP FOR THE EFFECTS OF OA ON THE COASTAL OCEAN

Shellfish growers are, by definition, environmentalists, because their livelihood depends entirely on the health of the coastal ocean. However, a cross section of oyster farmers is unlikely to reveal a number of outspoken environmental activists. Rather, the industry is typified by dedicated businessmen who would much rather put their heads down and work than participate in environmental advocacy. However, OA has leapt suddenly out of hypothetical discussions for the future and into the day-to-day life of shellfish growers—who now recognize a very clear and immediate threat to their industry and possess a fairly advanced level of understanding of acidification and the coastal processes affecting it (Mabardy, 2014). A recent survey found that over 50% of the those in the West Coast industry have personal experience with effects of OA, and 75% were very or extremely concerned about OA (Mabardy, 2014). There is hope among the industry, however, in that 59% of respondents indicated they believed they were definitely or somewhat able to adapt to OA.


The direct effects of OA on shellfish larval shell formation are troubling to shellfish growers, wild harvest fishermen, and to many other groups concerned about the health of shell-forming organisms. However, the more complex, and indirect, effects of OA on the general health of coastal systems are even more disconcerting to the Pacific Northwest shellfish industry. Reports of

seed mortality in commercial nurseries become more widespread each season and are likely related to the challenging conditions seed experience once they leave the protected waters of commercial hatcheries. While building capacity for buffering of remote setting tanks at commercial farms should provide some resiliency, as early post-metamorphic stages of bivalves appear to be more sensitive to acidification than later juveniles (Waldbusser et al., 2010), at some point demands for algal production and infrastructure require out-planting. The Pacific Northwest shellfish industry cannot treat the entire coastal ocean, and the general deterioration of coastal water quality is a pressing concern for the entire industry.

Growers understand that development of treatment systems and new hatchery capacity are only stopgap measures, and the only real solution to OA is to address its causes. This puts shellfish farmers in a unique position, as business owners depend on fossil fuels to maintain their livelihood, yet also heavily depend on the health of the coastal ocean to produce sensitive shellfish species. A visit to any shellfish hatchery in the Pacific Northwest will reveal thousands of gallons of diesel or propane fuel on site, used to heat seawater for larvae production. Hatchery managers work within a paradox of simultaneously releasing CO₂ into the atmosphere, which exacerbates OA, and adding carbonate to seawater to repair it. However, the fact that shellfish growers live and work in the real, fossil-fuel-dominated world makes the industry an important voice in the discussion to slow the advance of OA worldwide.

Industry representatives now devote a great deal of time and energy to discussing coastal OA's impacts on the Pacific Northwest shellfish industry (Bill Dewey, Taylor Shellfish Farms, *pers. comm.*, December 4, 2014). Industry involvement has helped expand the discussion of acidification management from the single issue of global carbon reduction to include practical actions that can be taken at the local level to reduce and

mitigate acidification effects. These local decision makers are fundamentally different entities, with fundamentally different science questions, than the groups interested in international-scale discussions of carbon inputs to the atmosphere. The direct involvement of shellfish industry representatives has contributed significantly to a growing body of literature that outlines strategies by which management actions can be targeted toward reducing the effects of OA at the local level (e.g., Kelly et al., 2011; Washington State Blue Ribbon Panel on Ocean Acidification, 2012; Strong et al., 2014).

Shellfish industry outreach efforts have paired effectively with regional not-for-profit organizations (<http://sustainablefish.org/global-programs/global-ocean-health>), with the primary focus of making direct contact with shellfish growers and fishermen, not only in the Northwest but also on the US East Coast and throughout the world. Recent workshops regarding the Gulf of Maine, Chesapeake Bay, Mexico, and New Zealand have brought together industry representatives, policymakers, and researchers, and have yielded similar results: growers and fishermen throughout all these regions are very concerned about potential impacts of OA on their industry and are universally interested in the role water quality monitoring can play in helping their industry face these challenges. In this way, the shellfish industry acts as a bridging organization between scientists, policymakers, and other stakeholders. By building consensus among those who work around and depend on a healthy ocean for their livelihood and the urban diners who consume their products, shellfish growers can contribute a powerful voice to discussions of OA and influence the difficult decisions necessary to halt its advance in the global ocean. 

ACKNOWLEDGEMENTS. The authors would like to acknowledge the determination of Robin Downey, Bill Dewey, Margaret Barrette, and Connie Smith in finding, and maintaining, funding for the PCSGA Monitoring Program. We thank the Washington governor's office and state legislature, and in particular Sen. Maria Cantwell, for their vision in understanding

the importance of coastal monitoring to West Coast shellfish growers, and their continued support for OA monitoring in the Pacific Northwest. We owe special thanks to the Oregon Coastal Caucus, and Sen. Betsy Johnson, for their tenacious support of Whiskey Creek Shellfish Hatchery, the Molluscan Broodstock Program, and the Oregon shellfish industry at large. We would like to recognize Brad Warren, Todd Capson, and Amy Grondin from the Sustainable Fisheries Partnership for their role in raising awareness of OA's impacts on shellfish in the Pacific Northwest and for building a bridge between hatchery managers, commercial fishermen, and resource managers across the United States and around the globe. We acknowledge the efforts of Diane Pleschner-Steele and Bruce Steele for their role in broadening the discussion to include OA's impacts on valuable wild fisheries, and in helping to bring together scientists, shellfish growers, commercial fishermen, and resource managers to form and sustain the California Current Acidification Network (C-CAN). We would like to express thanks to Bill Robertson (Seattle Aquarium, retired) for his practical insight into the design of commercial scale water treatment systems. We acknowledge funding support from the National Oceanic and Atmospheric Administration (NOAA)'s Ocean Acidification Program and NOAA's Pacific Marine Environmental Laboratory (PMEL contribution number 4268).

REFERENCES

- Alin, S.R., R.A. Feely, A.G. Dickson, J.M. Hernández-Ayón, L.W. Juranek, M.D. Ohman, and R. Goericke. 2012. Robust empirical relationships for estimating the carbonate system in the southern California Current System and application to CalCOFI hydrographic cruise data (2005–2011). *Journal of Geophysical Research* 117, C05033, <http://dx.doi.org/10.1029/2011JC007511>.
- Banas, N.S., B.M. Hickey, J.A. Newton, and J.L. Ruesink. 2007. Tidal exchange, bivalve grazing, and patterns of primary production in Willapa Bay, Washington, USA. *Marine Ecology Progress Series* 341:123–139, <http://dx.doi.org/10.3354/meps341123>.
- Brown, C.A., and J.H. Power. 2011. Historic and recent patterns of dissolved oxygen in the Yaquina estuary (Oregon, USA): Importance of anthropogenic activities and oceanic conditions. *Estuarine, Coastal, and Shelf Science* 92:446–455, <http://dx.doi.org/10.1016/j.ecss.2011.01.018>.
- Barton, A., B. Hales, G.G. Waldbusser, C. Langdon, and R.A. Feely. 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, <http://dx.doi.org/10.4319/lo.2012.57.3.0698>.
- Bednaršek, N., R.A. Feely, J.C.P. Reum, B. Peterson, J. Menkel, S.R. Alin, and B. Hales. 2014. *Limacina helicina* shell dissolution as an indicator of declining habitat suitability due to ocean acidification in the California Current Ecosystem. *Proceedings of the Royal Society B*, <http://dx.doi.org/10.1098/rspb.2014.0123>.
- Bednaršek, N., G.A. Tarling, D.C.E. Bakker, S. Fielding, E.M. Jones, H.J. Venables, P. Ward, A. Kuzirian, B. Lézé, R.A. Feely and E.J. Murphy. 2012. Extensive dissolution of live pteropods in the Southern Ocean. *Nature Geoscience* 5:881–885, <http://dx.doi.org/10.1038/ngeo1635>.
- Chan, F., J.A. Barth, J. Lubchenko, A. Kirincich, H. Weeks, W.T. Peterson, and B.A. Menge. 2008. Emergence of anoxia in the California current large marine ecosystem. *Science* 319:920, <http://dx.doi.org/10.1126/science.1149016>.
- Dumbauld, B.R., B.E. Kauffmann, A.C. Trimble, and J.L. Ruesink. 2011. The Willapa Bay oyster reserves in Washington State: Fishery collapse, creating a sustainable replacement, and the potential for habitat conservation and restoration. *Journal of Shellfish Research* 30:71–83, <http://dx.doi.org/10.2983/035.030.0111>.
- Elston, R.A., H. Hasegawa, K.L. Humphrey, I.K. Polyak, and C.C. Häse. 2008. Re-emergence of *Vibrio tubishii* in bivalve shellfish aquaculture: Severity, environmental drivers, geographic extent and management. *Diseases of Aquatic Organisms* 82:119–134, <http://dx.doi.org/10.3354/dao01982>.
- Fabry, V.J., B.A. Seibel, R.A. Feely, and J.C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science* 65:414–432, <http://dx.doi.org/10.1093/icesjms/fsn048>.
- Feely, R.A., S.R. Alin, J. Newton, C.L. Sabine, M. Warner, A. Devol, C. Krembs, and C. Maloy. 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. *Estuarine, Coastal, and Shelf Science* 88:442–449, <http://dx.doi.org/10.1016/j.ecss.2010.05.004>.
- Feely, R.A., C.L. Sabine, J.M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive “acidified” water onto the continental shelf. *Science* 320:1490–1492, <http://dx.doi.org/10.1126/science.1155676>.
- Feely, R.A., T. Klinger, J.A. Newton, and M. Chadsey. 2012a. *Scientific Summary of Ocean Acidification in Washington State Marine Waters*. NOAA OAR Special Report.
- Feely, R.A., C.L. Sabine, R.H. Byrne, F.J. Miller, A.G. Dickson, R. Wanninkhof, A. Murata, L.A. Miller, and D. Greeley. 2012b. *Global Biogeochemical Cycles* 26(3), GB3001, <http://dx.doi.org/10.1029/2011GB004157>.
- Frankignoulle, M., G. Abril, A. Borges, I. Bourge, C. Canon, B. Delille, E. Libert, and J.M. Theate. 1998. Carbon dioxide emission from European estuaries. *Science* 282:434–436, <http://dx.doi.org/10.1126/science.282.5388.434>.
- Gaylord, B., K.J. Kroeker, J.M. Sunday, K.M. Anderson, J.P. Barry, N.E. Brown, S.D. Connell, S. Dupont, K.E. Fabricius, J.M. Hall-Spencer, and others. 2014. Ocean acidification through the lens of ecological theory. *Ecology* 96:3–15, <http://dx.doi.org/10.1890/14-0802.1>.
- Gazeau, F., L.M. Parker, S. Comeau, J.-P. Gattuso, W.A. O'Connor, S. Martin, H.-O. Pörtner, and P.M. Ross. 2013. Impacts of ocean acidification on marine shelled molluscs. *Marine Biology* 160:2,207–2,245, <http://dx.doi.org/10.1007/s00227-013-2219-3>.
- Gordon, D.G., and N.E. Blanton. 2001. *Heaven on the Half Shell: The Story of the Northwest's Love Affair with the Oyster*. Washington Sea Grant, Seattle, WA, and WestWinds Press, Portland, OR.
- Green, M.A., G.G. Waldbusser, S.L. Reilly, K. Emerson, and S. O'Donnell. 2009. Death by dissolution: Sediment saturation state as a mortality factor for juvenile bivalves. *Limnology and Oceanography* 54:1,037–1,047, <http://dx.doi.org/10.4319/lo.2009.54.4.1037>.
- Gruber, N., C. Hauri, Z. Lachkar, D. Loher, T.L. Frölicher, and G.-K. Plattner. 2012. Rapid progression of ocean acidification in the California current system. *Science* 337:220–223, <http://dx.doi.org/10.1126/science.1216773>.
- Hales, B., L. Karp-Boss, A. Perlin, and P. Wheeler. 2006. Oxygen production and carbon sequestration in an upwelling coastal margin. *Global Biogeochemical Cycles* 20, GB3001, <http://dx.doi.org/10.1029/2005GB002517>.

- Hales, B., T. Takahashi, and L. Bandstra. 2005. Atmospheric CO₂ uptake by a coastal upwelling system. *Global Biogeochemical Cycles* 19, GB1009, <http://dx.doi.org/10.1029/2004GB002295>.
- Harris, K.E., M.D. DeGrandpre, and B. Hales. 2013. Aragonite saturation state dynamics in a coastal upwelling zone. *Geophysical Research Letters* 40:2,720–2,725, <http://dx.doi.org/10.1002/grl.50460>.
- Hauri, C., N. Gruber, C.-K. Plattner, S. Alin, R.A. Feely, B. Hales, and P.A. Wheeler. 2009. Ocean acidification in the California Current System. *Oceanography* 22(4):60–71, <http://dx.doi.org/10.5670/oceanog.2009.97>.
- Hauri, C., N. Gruber, A.M.P. McDonnell, and M. Vogt. 2013. The intensity, duration, and severity of low aragonite saturation state events on the California continental shelf. *Geophysical Research Letters* 40:3,424–3,428, <http://dx.doi.org/10.1002/grl.50618>.
- Hettinger, A., E. Sanford, T.M. Hill, A.D. Russell, K.N.S. Sato, J. Hoey, M. Forsch, H.N. Page, and B. Gaylord. 2012. Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. *Ecology* 93:2,758–2,768, <http://dx.doi.org/10.1890/12-05671>.
- Hinga, K. R. 1992. Co-occurrence of dinoflagellate blooms and high pH in marine enclosures. *Marine Ecology Progress Series* 86:181–187, <http://www.int-res.com/articles/meps/86/m086p181.pdf>.
- Hofmann, G.E., J.P. Barry, P.J. Edmunds, R.D. Gates, D.A. Hutchins, T. Klinger, and M.A. Sewell. 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: An organism-to-ecosystem perspective. *Annual Review of Ecology, Evolution, and Systematics* 41:127–147, <http://dx.doi.org/10.1146/annurev.ecolsys.110308.120227>.
- Juranek, L.W., R.A. Feely, W.T. Peterson, S.R. Alin, B. Hales, J. Peterson, K. Lee, and C.L. Sabine. 2009. A novel method for determination of aragonite saturation state on the continental shelf of central Oregon using multi-parameter relationships with hydrographic data. *Geophysical Research Letters* 37, L01601, <http://dx.doi.org/10.1029/2009GL040778>.
- Kelly, R.P., M.M. Foley, W.S. Fisher, R.A. Feely, B.S. Halpern, G.G. Waldbusser, and M.R. Caldwell. 2011. Mitigating local causes of ocean acidification with existing laws. *Science* 332:1,036–1,037, <http://dx.doi.org/10.1126/science.1203815>.
- Kroeker, K.J., R.L. Kordas, R. Crim, I.E. Hendriks, L. Ramajo, G.S. Singh, C.M. Duarte, and J.-P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. *Global Change Biology* 19:1,884–1,896, <http://dx.doi.org/10.1111/gcb.12179>.
- Kroeker, K.J., R.L. Kordas, R.N. Crim, and G.G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecology Letters* 13:1,419–1,434, <http://dx.doi.org/10.1111/j.1461-0248.2010.01518.x>.
- Kurihara, H., S. Kato, and A. Ishimatsu. 2007. Effects of increased seawater pCO₂ on early development of the oyster *Crassostrea gigas*. *Aquatic Biology* 1:91–98, <http://dx.doi.org/10.3354/ab00009>.
- Mabardy, R. 2014. Exploring perceptions and experiences of the U.S. West Coast shellfish industry dealing with ocean acidification. Master's Thesis, Oregon State University, Corvallis, OR.
- McLaughlin, K., S.B. Weisberg, A.G. Dickson, G.E. Hofmann, J.A. Newton, D. Aseltine-Neilson, A. Barton, S. Cudd, R.A. Feely, I.W. Jefferds, and others. 2015. Core principles of the California Current Acidification Network: Linking chemistry, physics, and ecological effects. *Oceanography* 28(2):160–169, <http://dx.doi.org/10.5670/oceanog.2015.39>.
- Miller, A.W., A.C. Reynolds, C. Sobrino, and G.F. Riedel. 2009. Shellfish face uncertain future in high CO₂ world: Influence of acidification on oyster larvae calcification and growth in estuaries. *PLoS ONE* 4:e5661, <http://dx.doi.org/10.1371/journal.pone.0005661>.
- Pörtner, H.O. 2008. Ecosystem effects of ocean acidification in times of ocean warming: A physiologist's view. *Marine Ecology Progress Series* 373:203–217, <http://dx.doi.org/10.3354/meps07768>.
- Ringwood, A.H., and C.J. Keppler. 2002. Water quality variation and clam growth: Is pH really a non-issue in estuaries? *Estuaries* 25:901–907, <http://dx.doi.org/10.1007/BF02691338>.
- Ruesink, J.L., C. Roegner, B.R. Dumbauld, J. Newton, and D.A. Armstrong. 2003. Contributions of coastal and watershed energy sources to secondary production in a northeastern Pacific estuary. *Estuaries* 26:1,079–1,093, <http://dx.doi.org/10.1007/BF02803365>.
- Rykaczewski, R.R., and J.P. Dunne. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophysical Research Letters* 37, L21606, <http://dx.doi.org/10.1029/2010GL045019>.
- Southern California Coastal Water Research Project. 2010. *Ocean Acidification Impacts on Shellfish Workshop: Findings and Recommendations*. Technical Report 624, Southern California Coastal Water Research Project, Costa Mesa, CA.
- Strong, A.L., K.J. Kroeker, L.T. Teneva, L.A. Mease, and R.P. Kelly. 2014. Ocean acidification 2.0: Managing our changing coastal ocean chemistry. *BioScience* 64:581–592, <http://dx.doi.org/10.1093/biosci/biu072>.
- Talmage, S.C., and C.J. Gobler. 2011. Effects of elevated temperature and carbon dioxide on the growth and survival of larvae and juveniles of three species of Northwest Atlantic bivalves. *PLoS ONE* 6(10):e26941, <http://dx.doi.org/10.1371/journal.pone.0026941>.
- Waldbusser, G.G., H. Bergschneider, and M.A. Green. 2010. Size-dependent pH effect on calcification in post-larval hard clam *Mercentaria* spp. *Marine Ecology Progress Series* 417:171–182, <http://dx.doi.org/10.3354/meps08809>.
- Waldbusser, G.G., E.L. Brunner, B.A. Haley, B. Hales, C.J. Langdon, and F.G. Prahl. 2013. A developmental and energetic basis linking larval oyster shell formation to acidification sensitivity. *Geophysical Research Letters* 40:2,171–2,176, <http://dx.doi.org/10.1002/grl.50449>.
- Waldbusser, G.G., and J.E. Salisbury. 2014. Ocean acidification in the coastal zone from an organism's perspective: Multiple system parameters, frequency domains, and habitats. *Annual Review of Marine Science* 6:221–247, <http://dx.doi.org/10.1146/annurev-marine-121211-172238>.
- Waldbusser, G.G., B. Hales, C.J. Langdon, B.A. Haley, P. Schrader, E.L. Brunner, M.W. Gray, C.A. Miller, and I. Gimenez. 2015. Saturation-state sensitivity of marine bivalve larvae to ocean acidification. *Nature Climate Change* 5:273–280, <http://dx.doi.org/10.1038/nclimate2479>.
- Washington State Blue Ribbon Panel on Ocean Acidification. 2012. *Ocean Acidification: From Knowledge to Action, Washington State's Strategic Response*. H. Adelman and L. Whitely Binder, eds, Washington Department of Ecology, Olympia, Washington, Publication no. 12-01-015.
- Wootton, J.T., C.A. Pfister, and J.D. Forester. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proceedings of the National Academy of Sciences of the United States of America* 105:18,848–18,853, <http://dx.doi.org/10.1073/pnas.0810079105>.

AUTHORS. Alan Barton (alan_barton22@yahoo.com) is Production Manager and Research Coordinator, Whiskey Creek Shellfish Hatchery, Tillamook, OR, USA. George G. Waldbusser is Assistant Professor, Oregon State University, Corvallis, OR, USA. Richard A. Feely is Senior Scientist, National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, Seattle, WA, USA. Stephen B. Weisberg is Executive Director, Southern California Coastal Water Research Project Authority, Costa Mesa, CA, USA. Jan A. Newton is Affiliate Assistant Professor, University of Washington, Seattle, WA, USA. Burke Hales is Professor, Oregon State University, Corvallis, OR, USA. Sue Cudd is Owner, Whiskey Creek Shellfish Hatchery, Tillamook, OR, USA. Benoit Eudeline is Chief Hatchery Scientist, Taylor Shellfish Hatchery, Quilcene, WA, USA. Chris J. Langdon is Professor, Oregon State University, Newport, OR, USA. Ian Jefferds is General Manager, Penn Cove Shellfish, Coupeville, WA, USA. Teri King is Marine Water Quality Specialist, Washington Sea Grant, Shelton, WA, USA. Andy Suhrbier is Senior Biologist, Pacific Shellfish Institute, Olympia, WA, USA. Karen McLaughlin is Biogeochemist, Southern California Coastal Water Research Project Authority, Costa Mesa, CA, USA.

ARTICLE CITATION

Barton, A., G.G. Waldbusser, R.A. Feely, S.B. Weisberg, J.A. Newton, B. Hales, S. Cudd, B. Eudeline, C.J. Langdon, I. Jefferds, T. King, A. Suhrbier, and K. McLaughlin. 2015. Impacts of coastal acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented in response. *Oceanography* 28(2):146–159, <http://dx.doi.org/10.5670/oceanog.2015.38>.