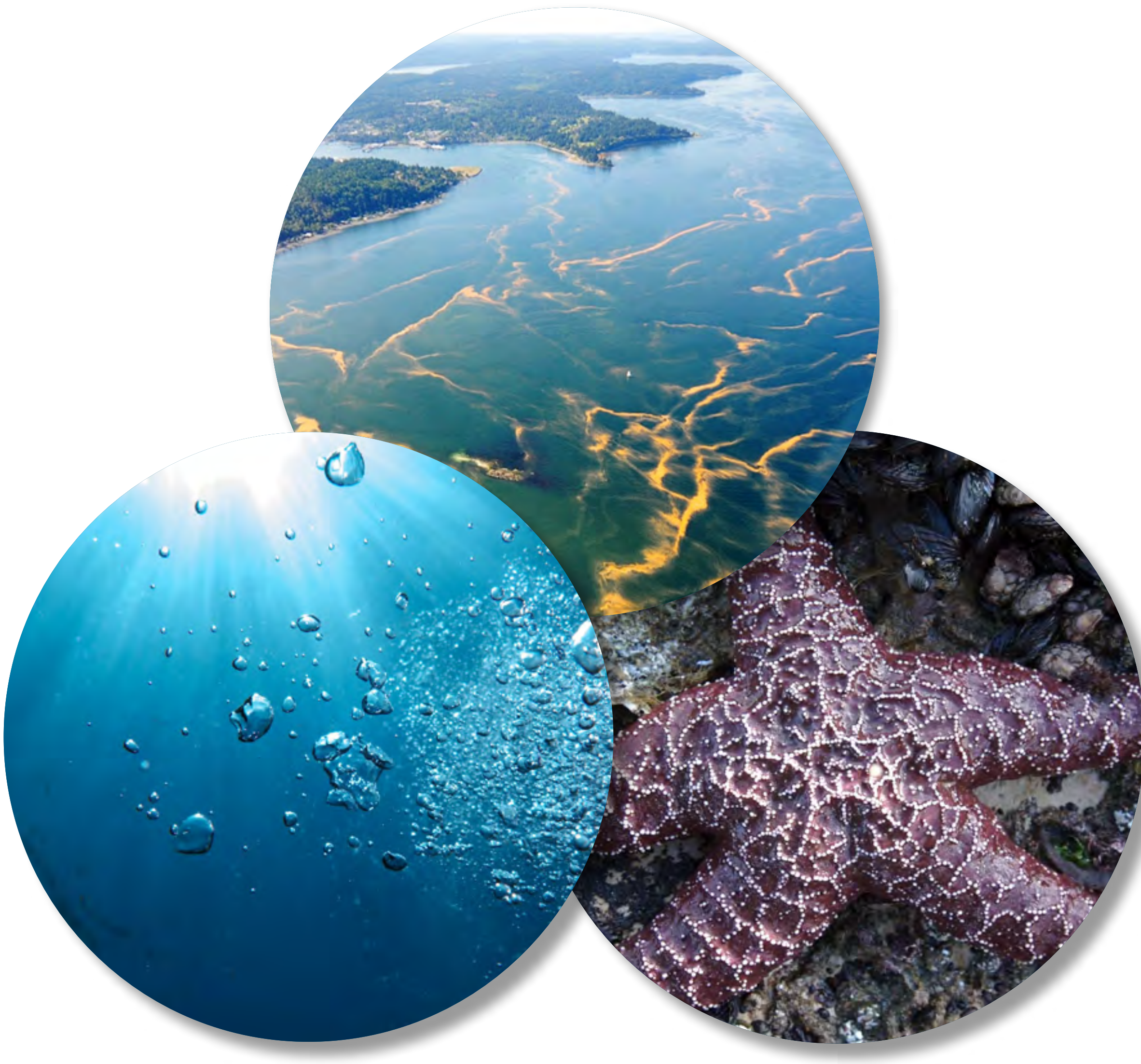
Oxygen for life

Understanding how low dissolved oxygen in Puget Sound affects marine ecosystems



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Science advisors
Joel Baker, Director, Puget Sound Institute, University of Washington Tacoma
Stefano Mazzilli, Senior Research Scientist, Puget Sound Institute, University of Washington Tacoma

Editorial contributors
Sarah DeWeerdt, Freelance Science Writer
Christopher Dunagan, Senior Writer
Marielle Kanojia, Engagement Strategist
Sylvia Kantor, Designer and Editor
Jeff Rice, Managing Editor

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Cover photos
Clockwise from top: Red-orange streaks of an extensive algal bloom (Noctiluca) in Puget Sound seen during the summer of 2015. Eyes Over Puget Sound/Ecology (CC BY-NC 2.0); Purple seastar. Photo: Jerry Kirkhart (CC BY 2.0). Bottom: Ocean bubbles. Photo: John Turnbull (CC BY-NC-SA 2.0)

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Introduction

This publication grew out of a series of workshops exploring the science of dissolved oxygen in Puget Sound. It comes at a time when managers and policy makers are faced with tough questions about the future of one of marine life's fundamental needs.

Studies show that impacts such as global warming will gradually change the amount of dissolved oxygen available to marine life in Puget Sound. Mathematical models also suggest that other human impacts such as the release of nitrogen from wastewater treatment plants, agriculture, and stormwater will have an impact as well.

Part of our goal with the workshop series is to simply understand what we know and don't know about these conditions. The articles in these pages, especially section one, explore some of the fundamentals. They are designed to help non-experts understand the causes of low dissolved oxygen—such as algal blooms fed by excess nitrogen—as well as when, where and why oxygen levels are changing.

We also explore questions that may be harder to answer. Questions that are puzzling scientists. Chief among them is how much humans might tip the balance. Will excess nitrogen released from human wastewater, for example, cause a significant impact on Puget Sound's species? The answers may affect state and federal regulations and could lead to billions of dollars in retrofits to wastewater treatment plants.

At the heart of these questions is a fundamental fact about Puget Sound: it is already naturally low in oxygen. Even under the best of circumstances, at certain times of the year, parts of Puget Sound will be in violation of dissolved oxygen requirements. That is because of Puget Sound's natural shape—there are areas where water doesn't circulate as well—and because of the input of water from the ocean that also carries with it loads of oxygen-depleting nitrogen. In fact, 88% of all nitrogen in Puget Sound comes from ocean sources, including waters from outside Washington. Another 3% of the nitrogen comes from natural watershed sources.

That leaves a remaining 9% from human sources including agriculture, wastewater treatment plants, and stormwater runoff. Modeling suggests those extra nutrients may further decrease dissolved oxygen in parts of Puget Sound, but we know that this is highly variable in space and time. There may be pockets of Puget Sound that experience low dissolved oxygen levels, but not others. Whether significant changes to dissolved oxygen will harm marine life depends upon when and where different species occur and how they are able to respond. Section two of this booklet includes a framework prepared by University of Washington biologist Tim Essington by which to analyze these potential impacts.

Finally, in sections three and four we look at regulatory concerns and analyze some of the tradeoffs facing policy makers as they weigh the potential needs of future nutrient management. We close with the inevitable concerns posed by global warming. As our workshop series continues, the University of Washington Puget Sound Institute is collaborating with experts locally and globally to advance the science to inform these important decisions.

1

How nutrients lead to low dissolved oxygen

Much of life on Earth, whether on land or in the water, requires oxygen to survive. In marine environments, oxygen is absorbed directly from the atmosphere and from aquatic plants undergoing photosynthesis. When oxygen levels become especially low, a dangerous condition known as hypoxia can occur. Hypoxia refers to conditions in which the concentration of oxygen falls to levels that can harm or kill organisms. This section addresses some of the basics of low dissolved oxygen as well as potential causes, including excess nitrogen from both natural and human sources. Questions about the level of human impacts on dissolved oxygen will have big policy implications (see section 3 "Regulatory concerns") as regulators seek to determine how much nitrogen to release from local wastewater treatment plants.

Understanding the causes of low dissolved oxygen in Puget Sound

Plankton bloom near Edmonds, Washington. Photo: Washington State Department of Ecology

At certain times of the year, Puget Sound is naturally low in dissolved oxygen. This is caused largely because of the shape of the basin and the chemistry of the water coming in from the ocean. Ocean water arrives in a form that is both poorly oxygenated and full of nutrients. Under the right conditions, those nutrients can trigger algal blooms that further deplete the water of oxygen.

Takeaways

- Excess nitrogen triggers plankton blooms leading to oxygen depletion through bacterial decomposition.
- Ocean sources contribute 88% of Puget Sound's nitrogen, while human activities provide 2.6 times more than natural land sources.
- Summer conditions create ideal environments for oxygen depletion.
- Low-oxygen areas occur mainly in deep, isolated waters like Hood Canal and shallow embayments in South Puget Sound, and east of Whidbey Island.
- Incoming seawater is low in dissolved oxygen.

THE course of events that trigger low-oxygen conditions in Puget Sound is fairly well understood. A key factor involves excess nutrients, particularly nitrogen, that over-feed a large variety of plankton drifting through the water. When large numbers of these tiny organisms die and decay, the bacterial activity consumes available oxygen, which can lead to unhealthy or even lethal levels of oxygen affecting marine creatures.

It's a balancing act within a Puget Sound food web that depends on the growth of phytoplankton, tiny microalgae and plants that can generate their own energy from nutrients and sunlight. Phytoplankton are eaten by larger marine organisms, which are eaten by others in turn, and so on, up the food web. Organic carbon as well as nitrogen cycling through the food web may affect oxygen levels.

In proper balance, nitrogen is an essential ingredient in the diversity of life that exists in Puget Sound. Still, too much nitrogen can lead to massive plankton blooms, producing an overabundance of food that exceeds the consumptive capacity of higher organisms. When that happens, bacteria take over to break down the surplus biomass, which can lead to low-oxygen conditions.

While human sources of nitrogen may tip the balance, scientists point out that natural sources of nitrogen are abundant throughout Puget Sound. Alder trees and other nitrogen-fixing plants, along with wildlife contribute nitrogen to forest soils. These upland nitrogen sources, along with decaying plants and dead salmon, can make their way into streams before reaching Puget Sound. Even larger amounts of nitrogen circulate in the Pacific Ocean and enter Puget Sound through the Strait of Juan de Fuca. It is estimated that 88% of the nitrogen in Puget Sound comes from the ocean sources.

From the land, human sources contribute about 2.6 times more nitrogen than natural sources, according to Ecology estimates. But the story becomes complicated by issues of time and location. When and where nitrogen enters Puget Sound can make all the difference. For example, winter months bring less sunlight and cooler temperatures to slow the growth of phytoplankton. At the same time, winter storms increase the mixing of fresh and salt waters, reducing the nitrogen concentration. Higher river flows in winter help to carry nitrogen out of Puget Sound.

In contrast, the sunny days of summer encourage the growth of plankton in the surface waters of Puget Sound. Nitrogen carried into the Sound by freshwater tends to stay at the surface due to its lower density and less mixing. Nitrogen-laden effluent discharged from pipes tends to rise as well. During the relatively calm seas of summer, layers of water may form with distinct differences in temperature, density and biological activity, a process called stratification which can influence oxygen concentrations at different depths.

In many estuaries throughout the world, including Puget Sound, the outflow of freshwater at the surface is driven by river flows. The outflow is counterbalanced by an influx of heavier saltwater creeping inward from the ocean along the bottom, carrying waters that are naturally low in dissolved oxygen. Where the incoming, deep-moving saltwater encounters underwater ridges along the bottom, known as "sills," the heavier saltwater gets churned up and pushed toward the surface. This is how some of the nitrogen-rich ocean water reaches the sunlit layer—the euphotic zone—where phytoplankton are busily growing and multiplying.

Meanwhile, the powerful, unrelenting tides push and pull huge masses of water throughout Puget Sound, including every inlet and channel. Seen from shore, the waters rise and fall twice each day, as tidal currents carry the water in and out of the inlets and back and forth through the channels.

All of this goes to show that a multitude of dynamic water movements must be accounted for in computer models designed to predict oxygen levels. Among the key questions: How much of the nitrogen entering Puget Sound gets consumed by plankton? How much of the plankton gets broken down by bacteria? And how much oxygen gets used up, not just overall but in specific locations throughout the Sound.

Low-oxygen conditions, caused by decaying plankton, may also involve isolation from strong currents that carry highly oxygenated water. That's why low-oxygen areas tend to be found at depth in long, narrow waterways, such as southern Hood Canal, as well as the bays and inlets of South Puget Sound, along with the waters east of Whidbey Island—all known for their occasional hypoxic events that can harm marine life.

How low-oxygen waters affect life in the sea depends on the species as well as the speed at which adverse conditions arise. While fish often have time to swim away, massive fish kills can occur when strong winds suddenly blow away the surface waters, allowing low-oxygen waters to rise from the depths.

For bottom-dwelling organisms that move slowly or not at all—such as sea stars and geoduck clams—even occasional events of extremely low oxygen may prevent their populations from recovering, as seen in some areas of Hood Canal.

Low oxygen conditions also can lead to sub-lethal effects for sea life, such as reduced feeding, slower growth, and increased vulnerability to predation, as well as potential effects on reproductive and immune systems. ■

This article first appeared in *Salish Sea Currents Magazine.*

The ocean is a major source of naturally occurring nitrogen in Puget Sound but watershed sources including alder trees and decaying salmon carcasses also contribute nitrogen via streams. Human causes include wastewater treatment and agricultural runoff. Photos: Adobe Stock

The Strait of Juan De Fuca looking west at Cape Flattery.
Photo: Sam Beebe, Ecotrust (CC BY 2.0)

Where does most of Puget Sound's nitrogen come from?

If you ask people to name some of the rivers that flow into Puget Sound, they might list the Skagit or the Nisqually or any of the thousands of creeks and streams that arrive from the surrounding mountains. They are less likely to mention that Puget Sound's largest river is one you can't see from the land.

It's a river that has no name but starts deep off the Washington coast and pushes water through the Strait of Juan de Fuca in a raging torrent the size of the Amazon. This underwater Amazon flows through Juan de Fuca Canyon stirring up turbulent waves and eddies that churn the waters of Puget Sound deep below the surface.

This flow brings in life-giving nitrogen that feeds Puget Sound's creatures, from salmon to orcas. While this nitrogen, also known as a nutrient, is vital to a healthy Puget Sound, the large amount coming in from the ocean also makes the region more prone to algal blooms that can touch off naturally low oxygen conditions. About 88% of the nitrogen in Puget Sound is attributed to ocean sources.

Learn more about Puget Sound's underwater Amazon in *Salish Sea Currents Magazine*.

Download and share an infographic about sources of nitrogen in Puget Sound from the Encyclopedia of Puget Sound.

Sources of nitrogen in Puget Sound

What is nitrogen and why does it matter?

Nitrogen is a chemical element that is essential for the growth of all life on earth.

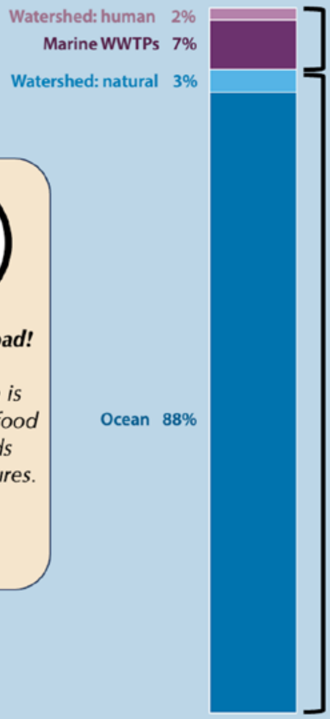
Known as a nutrient, it is a basic building block of the food web starting with algae (phytoplankton). But too much nitrogen can lead to low dissolved oxygen and other problems such as toxic algal blooms that can harm or kill aquatic organisms.

The addition of nitrogen from human activities can influence the timing, location, and size of algae blooms and by extension organisms' exposure to their effects.

As climate change warms the ocean, nitrogen is expected to increase and dissolved oxygen to decrease. At the same time, nitrogen from wastewater and agriculture may intensify as human populations grow.

Algae isn't all bad! *In fact, phytoplankton is the base of the food web that feeds many sea creatures. Too much can cause problems.*

Where does nitrogen in Puget Sound come from?



9% of nitrogen in Puget Sound is attributed to **human activity** in Washington State, primarily from wastewater treatment plants (WWTP), agriculture, and urban runoff.

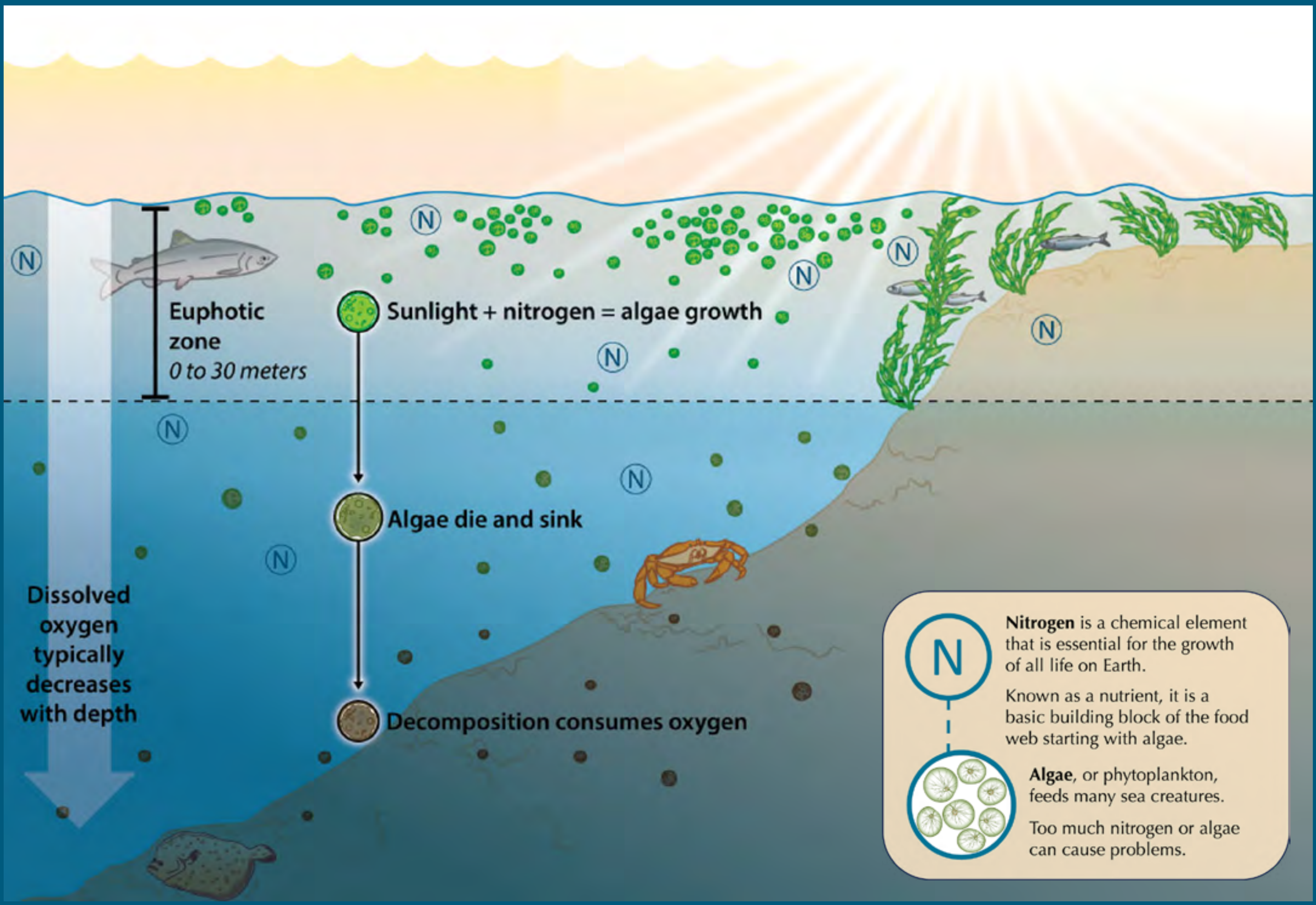
91% of nitrogen in Puget Sound comes from **watershed** and **ocean** sources

- 3% comes from Puget Sound watersheds via natural surface runoff to rivers
- 88% is attributed to ocean sources which includes both human and natural sources such as from Canada.
- < 1% comes from the atmosphere and groundwater.

Sources: Mohamedali et al. 2011; Mackas and Harrison 1997

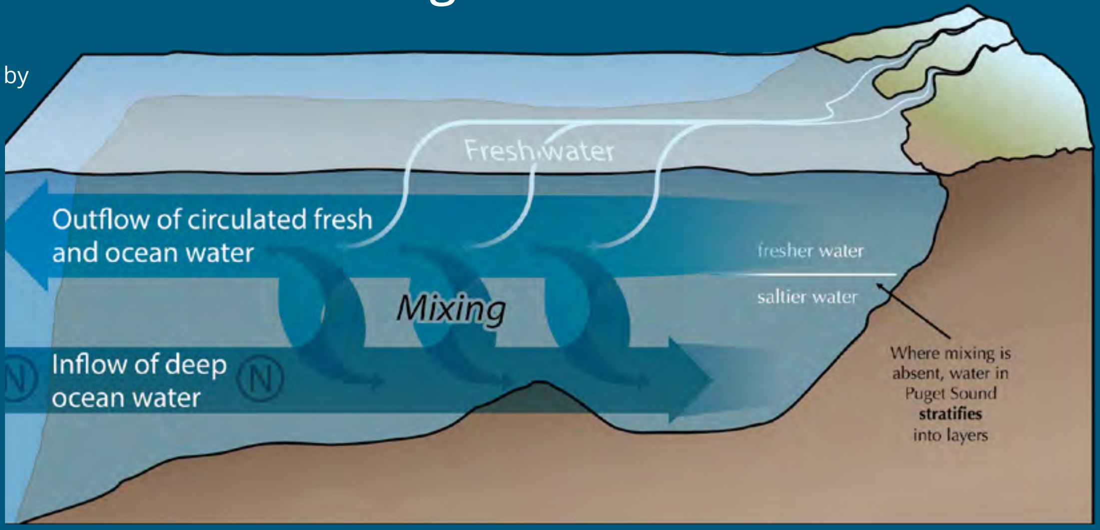
Excess nutrients can result in low dissolved oxygen

In Puget Sound, excess nitrogen plus sunlight triggers plankton blooms . As the algal plankton die and decay, they sink into deep water, where bacteria consume the available oxygen to break down them down. Known scientifically as eutrophication, this process of oxygen depletion is more likely in summer when sunlight, calm seas, and water stratification create the ideal conditions.



Circulation mixes and moves nitrogen

In Puget Sound, the outflow of freshwater at the surface, driven by river flows, is counter-balanced by an influx of heavier saltwater moving inward from the ocean along the bottom. Where the inflow of deep ocean water encounters underwater ridges, or "sills," along the bottom, the heavier saltwater gets pushed toward the surface. This is how some of the nitrogen-rich ocean water reaches the sunlit layer—the euphotic zone—where phytoplankton are busily growing and multiplying.



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Impacts on species

This section looks at the variety of ways that species in Puget Sound can respond to low oxygen conditions. Some, such as salmon and Dungeness crabs can move away from areas with low dissolved oxygen. Others, like Pacific herring can adapt like human runners training at high altitude. When hypoxia happens suddenly or when creatures like clams or other mud-dwelling invertebrates can't move away, organisms can suffocate and die. In our 'Ask a scientist' section, University of Washington biologist Tim Essington describes a framework to evaluate when and where low oxygen is likely to be problematic for aquatic life. The important thing to remember, he says, is that low dissolved oxygen is not always a problem in all situations. In fact, it often occurs naturally in Puget Sound. He argues that what matters most is whether a decrease in oxygen pushes levels below a species' unique threshold, and if so, when and where such exposure occurs.

Ask a scientist
How do you evaluate the effects of reduced oxygen on aquatic life?

Pacific herring (Clupea pallasii*).*
Photo: Daniel Moth/iNaturalist (CC BY-NC 4.0)

*There is an ongoing concern that human activities are causing a reduction in the amount of oxygen available to fish and invertebrates, particularly in Puget Sound. Scientists are working to evaluate when and where some of these reductions are likely to have an adverse ecological impact. As part of a series of workshops on Puget Sound water quality, we asked **Dr. Tim Essington** of the University of Washington School of Aquatic and Fishery Sciences to describe how low oxygen might affect species like salmon or Dungeness crabs. The following text is adapted from a video presentation by Essington in 2023.*

Takeaways

Tim Essington describes a three-part framework that can be used to evaluate when and where low oxygen is likely to be problematic for aquatic life.

- Oxygen problems are a matter of thresholds of species tolerance.
- Organisms have a range of responses available to them to try to cope with low dissolved oxygen.
- It matters when and where oxygen is depleted.

When is low dissolved oxygen problematic for species?

Low oxygen is only problematic when the oxygen level drops below certain thresholds. Those thresholds vary a great deal by species, but let's just take humans as an example. As you read this, maybe on your laptop in your home, or maybe in your office, you probably have plenty of oxygen in your room. Far more than you may actually need. Now let's say there is a 10% reduction in that oxygen. Maybe your room suddenly gets really crowded, and there are a lot of people competing for air. Because you started at a place where there is plenty of oxygen, you're probably not even going to notice that 10% reduction. It isn't enough to push oxygen levels low enough to a point where your body starts having trouble.

However, let's pretend that instead of reading this in the comfort of your office or in your home, you are halfway up Mount Everest. I have never climbed Mount Everest, but I suspect right around halfway up is probably where oxygen is getting really, really limiting. There may be just barely enough for you to be able to move and still maintain all your cognitive functions. Now, if there's a 10% reduction in that environment, that's a huge problem for you. So, when you start thinking about reductions, think about whether it is going to pass some threshold beyond which an organism is going to have challenges. What sort of challenges will it have coping with that new oxygen level?

A high altitude climber in the Himalayas. Photo Adobe Stock

How do species respond to low oxygen levels?

Organisms have a range of responses available to them to try to cope with thresholds of low oxygen. Typically, they can move, acclimate, or in the worst-case scenario, they may die.

The first response is an obvious one: ***If an animal has the capacity to move, it will move***. In Hood Canal, for example, typically what happens is oxygen becomes very depleted towards the end of the summer. This happens most often at the deepest parts of the waterway's southern end. Organisms may leave Hood Canal in one of two ways. They might just go north to try to get out of that whole region. And we do see some evidence that in fish. Or they simply might change how deep they are living. Crabs, for example, will move up into the shallows to try to avoid an area that has very, very low oxygen.

This is not to say that just because a species can move that there won't be a bad outcome. Presumably they were in that spot in the first place because that's where they wanted to be. Studies show that such a distribution shift can change a species' ability to find food or avoid predators, but it doesn't mean that they will simply die because the oxygen was below their threshold. They're going to do things to try to minimize their exposure.

Species may also acclimate to their surroundings. Herring and other animals can adopt physiological changes to cope with this new level of oxygen. It might be the structure of the gill itself will change to make it more efficient at pulling oxygen out of the water. The blood composition itself will change to enable it to be more effective at grabbing that oxygen than delivering it on to the rest of the fish tissue. Over many, many generations, you might start see evolution so particular species of fish, or perhaps a segment of a particular species of fish that lives in a particular environment, might start evolving the capacity to deal with low dissolved oxygen.

The last response is the one that we want to avoid: death. Death can happen when animals are unable to adopt any of those other coping mechanisms. And in fact, when we look at some of the fish kill events or any type of killing of marine life that happened due to low dissolved oxygen, it's often happening because the change in oxygen happened extremely abruptly, like in a matter of hours. In those cases, organisms didn't have the capacity to move or mount some sort of physiological ability to deal with that new condition.

*Pacific Hake (*Merluccius productus*), seen here at 115 feet in Puget Sound, can adopt physiological changes to cope low dissolved oxygen. Photo: Justin Warner/iNaturalist (CC BY-NC 4.0)*

Does it matter when and where oxygen is depleted?

Imagine a salmon wandering into Carkeek Creek to spawn. In most years, it's depositing and burying its eggs in the stream bed, so those eggs are living in the bottom of the creek in late autumn and winter. During that time, water needs to pass over the eggs and deliver fresh oxygen to them. Otherwise, they're going to suffocate. The overall amount of oxygen that's in Carkeek Creek in that period of time really, really matters to the survivorship of those eggs. The timing here is critical, because if there's a very low oxygen that happens in, say, July, that is not going to impact eggs that are only present much later in the year.

Now let's take salmon again, in this case migrating out into Puget Sound. While these salmon are in Puget Sound, they are inhabiting very shallow water. Very shallow water is typically extremely well oxygenated. For these salmon that are hanging out in the top, say, 15 or 20, feet of water, it really doesn't matter at all that at hundreds of feet below them resides really, really, low oxygen

Chum salmon spawning in Carkeek Creek, Seattle. Photo: Sdkevorkian/iNaturalist (CC BY-NC 4.0)

water, because they're not there. The spatial overlap of where the organism is and where the oxygen is low is incredibly important. We're not going to see a mass die-off of salmon that are at the surface because the bottom water is depleted in oxygen. And similarly, if there would happen to be perhaps a rapid intrusion of deep water with low dissolved oxygen into the surface waters, that would not be problematic for salmon if it happened after the salmon had already migrated through. So again, the time and place where oxygen passes those thresholds is incredibly important. ■

Video available at: https://youtu.be/fMjhV1GPNlg

Tim Essington is a fisheries ecologist and the director of the University of Washington School Aquatic and Fisheries Sciences.

Purple seastar. Photo: Jerry Kirkhart (CC BY 2.0)

How does dissolved oxygen affect species in Puget Sound?

Chronic stress from lack of oxygen can make aquatic organisms more vulnerable to disease, pollution, or predation. Low oxygen can also result in reduced habitat for some species.

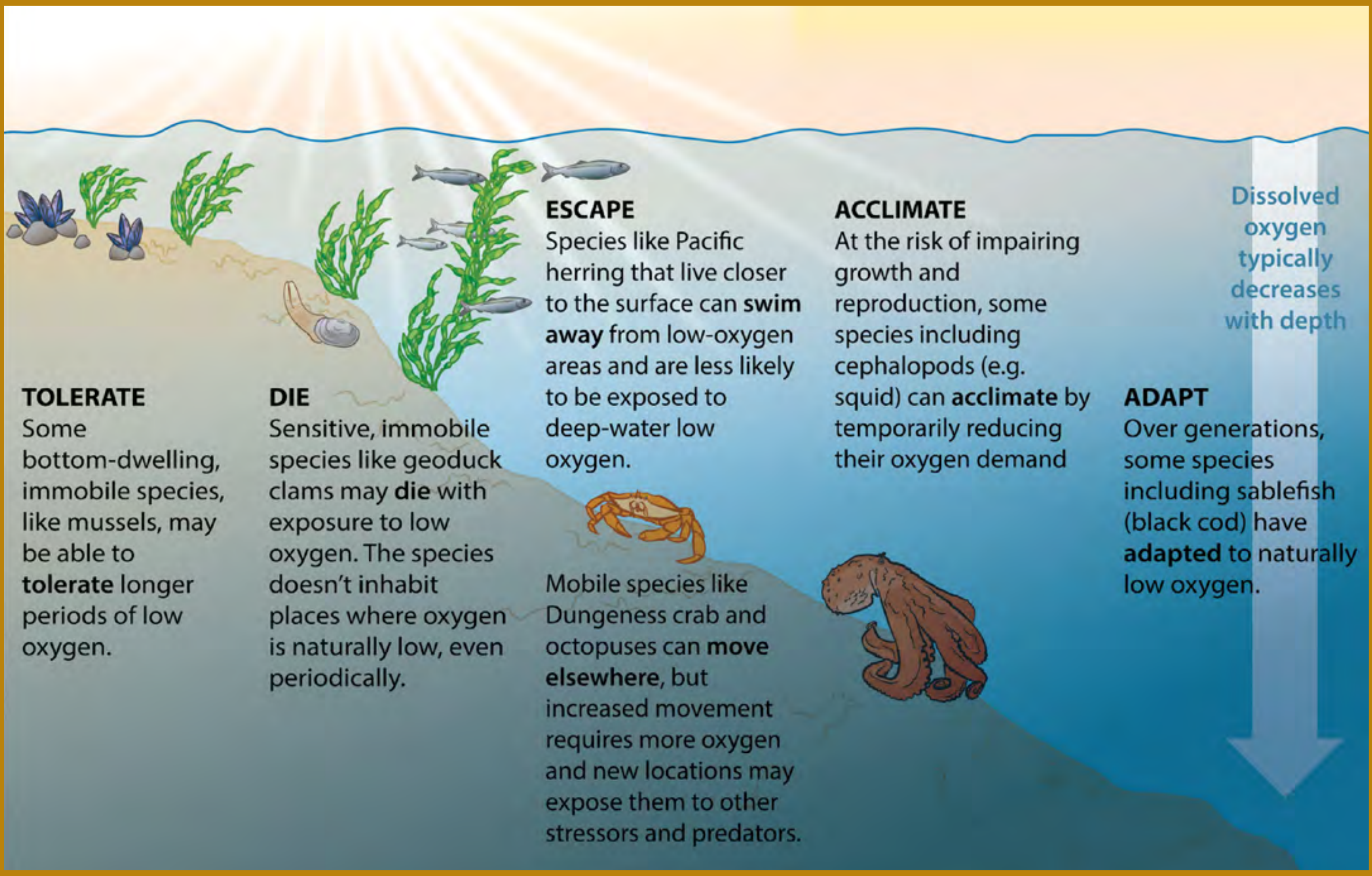
The most extreme impacts of low oxygen to aquatic organisms include decreased ability to reproduce, slowed development, deformities, and death. For some species, including squid, crabs, and octopuses it can impair eyesight.

Physiological changes can help some species survive but may come at a cost. Some fish, for example, can increase the surface area of their gills to allow more water (and thus more oxygen) to pass through. But this can increase the amount of pollution absorbed by their bodies. Other animals can increase their blood circulation or modify their need for energy.

- Too little dissolved oxygen can kill marine life or cause reduced growth and weakened immune systems.
- Mobile species can escape while stationary or slow-moving species suffer most in low-oxygen environments.
- Some species can acclimatize physiologically or adapt genetically over generations.

Mobility is a big advantage. Many species can move away to escape low oxygen conditions unless they are stationary like mollusks or anemones. Some species can temporarily acclimate, and others have adapted over generations to tolerate low oxygen. In more extreme cases, species can die, especially if the change in oxygen is sudden or they are exposed for too long.

Download and share infographic about how dissolved oxygen impacts aquatic life.



3

Regulatory concerns

At certain times of the year, many parts of Puget Sound are naturally low in oxygen. Chief causes are nitrogen and poorly oxygenated seawater flowing into Puget Sound from the Pacific Ocean. Nitrogen in particular is vital for the Puget Sound food web, but it also makes the region prone to algal blooms during warmer months that can deplete oxygen. These conditions, especially in places like Hood Canal and Puget Sound's bays and inlets can lead to a puzzle for regulators. What happens when natural conditions are lower than regulatory standards? And at what point do human-caused sources of nutrients from wastewater further impact these conditions? We explore these questions with an in-depth look at the struggle to determine dissolved oxygen standards for Puget Sound. These pages also include a probing look at when and where low dissolved oxygen is of most concern.

When are waters considered hypoxic?

An oxygen and temperature monitoring device fastened to a crab pot.
Photo: Jeremy Childress, OSU (CC BY-SA 2.0)

The search goes on for a set of definitions and thresholds to represent low-oxygen concentrations that threaten various aquatic creatures. Over the years, ecologists have relocated, reshaped and revised the word “hypoxia” to describe these conditions.

By Christopher Dunagan

Takeaways

- The term “hypoxia” originally described oxygen deficiency in humans, and later in the 1970s to describe oxygen-depleted water bodies that harm aquatic species.
- Research shows the commonly used standard of defining hypoxic conditions as 2 mg/L of dissolved oxygen is inadequate; many species experience lethal or sublethal effects at higher oxygen concentrations.
- Experts now reject a uniform definition of hypoxia, recognizing that oxygen thresholds vary greatly by species, life stage, and environmental conditions like temperature.

HYPOXIA, a word used to describe oxygen deficiency, first came into use in the medical field during studies of metabolic function in the 1940s. Hypoxia was seen as something occurring within the body of a human or animal that was not getting enough oxygen for normal function. During the 1970s, “hypoxia” also came to be widely used to describe bodies of water so depleted of oxygen that they were harming or even killing the aquatic species that lived there.

When discussing specific waterways, many researchers adopted a standard definition of hypoxia: a dissolved oxygen concentration of 2 milligrams per liter or less. This level was chosen for its observed effects on fish. But extensive research over the past five decades has shown that the effects of low oxygen vary greatly by species and local environmental conditions. Now, new definitions of hypoxia are emerging, and some researchers have stopped using the term altogether when referring to waterways.

The origins

The word “hypoxia” derives from the Greek “hypo,” meaning low, and “oxia,” as related to oxygen. A French scientist, Jean-Paul Richalet, traced the first use of the word in the United States to the year 1940, when it was adopted to describe low-oxygen conditions in human cardiology and anesthesiology. “Hypoxia” came to be preferred over varying degrees of “anoxia”—which literally means without any oxygen.

“The clinical distinction between anoxia (a life-threatening condition) and hypoxia (a condition where defense mechanisms can restore vital functions) was clearly defined by Carl Wiggers and Ralph Waters in 1941 and 1944, respectively,” according to Richalet. “However, ‘anoxia’ continued to be widely used in the 40s and 50s.

“The frequent use of expressions such as “progressive anoxia” or “moderate anoxia” suggests that scientists used “anoxia” with the meaning of “hypoxia,” not considering the prefix ‘a-’ as a total absence of oxygen,” he continued. “Finally, hypoxia took the lead in the ’60s with the development of cell biology and high-altitude physiology and medicine.”

While the word “hypoxia” was coming into general use within the medical field, marine biologists were using the term to describe low-oxygen conditions and its effects on all sorts of animals. In laboratory studies, researchers exposed various marine creatures to low-oxygen waters to observe the response. One common measure of severity, called LC50, describes the “lethal concentration” of oxygen (referring to a lethal lack of oxygen) in water that kills 50 percent of the test subjects.

Researchers recognized the importance of various behavioral and physiological changes taking place at reduced oxygen levels — generally well above levels that killed fish, shellfish or other creatures being studied. They also acknowledged that even the most sophisticated lab experiments bore only a slight resemblance to the real world, in which animals can move or otherwise respond to constantly changing conditions in the water.

An elusive number

Coming up with reliable numbers for low-oxygen effects on marine life remained an elusive challenge, as two Oregon State University researchers, Peter Doudoroff and Dean Shumway, reported in 1970 in a United Nations technical report.

“One does not need to study the literature very long to become convinced that there is indeed little agreement of reported findings," they wrote. "Minimum tolerable or 'threshold' levels of O2 reported by some investigators are several times greater than those reported by others for the same fish species, tested at about the same temperatures.

"Fish have been said by some to be capable and by others to be quite incapable of prompt detection and avoidance of low O2 concentrations," they said. "Reduction of O2 sometimes has been said to depress activity and sometimes to cause increases of the activity of fish... The reasons for these apparent contradictions have not been adequately explained."

The researchers reported on multiple studies that examined the effects of exposing fish to low-oxygen waters. They produced evidence showing that stressful—but not lethal—levels of oxygen can produce "chronic hypoxia" and eventual death through a "physiological disturbance that is different from the cause of death at rapidly lethal O2 levels," they said. Deadly levels of oxygen, they added, produced "acute hypoxia," in fish, keeping with the definition of hypoxia as a physiological condition.

Meanwhile, concerns were growing through the 1970s and '80s about the deteriorating condition of waterbodies throughout the United States. In 1985, the first "Nationwide Survey of Oxygen Depletion and Eutrophication in Coastal and Estuarine Waters" borrowed the term "hypoxia" from medicine and cellular biology to describe low-oxygen conditions found in natural waterways.

The authors did not define an oxygen level that would constitute hypoxia, but they used that term in reference to areas within waterways where people had observed and measured low-oxygen problems. They concluded that 38 percent of the nation's major estuaries were experiencing hypoxia, referring in some cases to violations of locally established water-quality criteria, such as 4 milligrams/liter.

The survey specifically identified waterways of concern throughout the United States, including Budd Inlet in southern Puget Sound, listed as a "priority hypoxic area." The report called out fish kills and oxygen levels as low as 1 mg/L in the inlet. Two

A massive die-off of Dungeness crab that washed up on Kalaloch Beach in 2022 was attributed to low oxygen levels. Photo: Jenny Waddell/NOAA

other Puget Sound areas, Port Susan near Whidbey Island and Lynch Cove in southern Hood Canal, were declared "potential hypoxic areas."

By 1986, multiple researchers, including Maurice Renaud of NOAA's Southwest Fisheries Science Center, were using the precise number 2 mg/L to describe "hypoxic" conditions in the Gulf of Mexico, with various effects noted at this oxygen concentration. A few other researchers chose other hypoxic levels for their studies, such as 2.5 mg/L or sometimes higher.

A wide range of levels

In 1992, NOAA's Office of Ocean Resources Conservation and Assessment (ORCA) launched a new program to better assess and compare the condition of estuaries nationwide, first collecting information in separate reports from five regions and then compiling a single national report. Eight parameters related to water quality were chosen for data gathering. To rank each parameter, specific thresholds were chosen. In the case of oxygen, "anoxia" was defined as 0 mg/L, "hypoxia" was between 0 and 2 mg/L, and "biological stress" was between 2 and 5 mg/L.

"The ranges were determined from nationwide data and from discussions with eutrophication experts," states the first report from the South Atlantic Region. "The thresholds used to classify ranges are designed to distinguish conditions among estuaries on a national basis and may not distinguish among estuaries within a region."

Concerns about low-oxygen conditions continued to grow for waterways throughout the country, as researchers reported an expansion of low-oxygen conditions in various waterways, while a new term, "dead zones," was being bandied about in newspapers and eventually adopted in scientific and government reports. In 1998, Congress passed the Harmful Algal Bloom and Hypoxia Research and Control Act, which called for increasing research on hypoxic conditions. The reports generally stuck with 2 mg/L as the definition of hypoxia for the sake of comparing waterways nationwide.

Neither the term "hypoxia" nor the use of 2 mg/L as a universal threshold came about without objections. In 1991, Richard Tyson and Tom Pearson with the Geological Society of London proposed new terminology in a publication that sparked discussion.

"Physiologists have long used the term 'hypoxia' to describe conditions or responses produced by stressful levels of oxygen deficiency," they wrote. "Its application to natural oxygen-deficient environments began to be common in the late 1970s, especially by those working in the Gulf of Mexico, and it is now in widespread use by marine biologists and ecologists.

"The term 'hypoxic' is also poorly defined," they said, "partly because the critical levels at which hypoxic responses are observed depend upon the taxa involved, and to a certain extent the environment. We recommend that 'hypoxic' and 'hypoxia' should be used only with respect to living (i.e. not fossil) organisms, and that only the other '-oxic' terms should be applied to describe the oxygen status of environments."

Removing "hypoxic" from their environmental lexicon, Tyson and Pearson proposed to keep "anoxic" for a zero level of oxygen and to use new terms, ranging from low to high concentrations: "suboxic" (0 to 0.2 ml/l), "dysoxic" (0.2 to 2 ml/l) and "oxic" (2 to 8 ml/l). Note that the units, milliliters per liter (ml/l) are used in place of the more common milligrams per liter (mg/L). For practical purposes, 1.0 ml/l equals 1.4 mg/L.

Although Tyson and Pearson's proposal generated debate and their paper is still cited today, their recommendations for new terminology did not gain widespread acceptance.

In 2008, two Spanish researchers, Raquel Vaquer-Sunyer and Carlos Duarte, took aim at the 2 mg/L threshold for hypoxia. They examined 872 published experiments involving 206 species reporting either oxygen thresholds or lethal limits. They found a huge variation in oxygen effects. At the high end, the median lethal oxygen concentration (LC50) was 8.6 mg/L for the sensitive larvae of Atlantic rock crab. At the other end of the scale, adult Eastern oysters survived anoxic (0 mg/L) conditions for a considerable period of time.

A commonly used threshold

The vast majority of studies, some 99 percent, used 2 mg/L as the experimental threshold when measuring how long organisms could survive at a low-oxygen level—even though most species in the studies showed lethal or sublethal effects at much higher concentrations, they said.

"Whereas the conventional 2 mg/L (threshold) may signal levels of hypoxia at which fisheries collapse, the results presented here show that it is inadequate as a threshold to conserve coastal biodiversity, because significant mortality would have already been experienced by many species," they concluded.

"In particular, most fish and crustaceans would be lost before the oxygen content of the waters reaches the threshold of 2 mg/L for these waters to be considered hypoxic by conventional criteria," they said. "Currently used thresholds of hypoxia are not conservative enough to avoid widespread mortality losses and need to be critically revised."

The two researchers proposed a "precautionary limit" of 4.6 mg/L, which would maintain populations for all but the most sensitive crab species and "effectively conserve marine biodiversity." Other thresholds, they added, could be applied to species at risk in specific waterways, taking into account potential differences between laboratory findings and natural conditions.

Two years later, in 2010, a team of six leading experts issued an exhaustive discussion of low-oxygen dynamics with a summary of low-oxygen conditions throughout the world. They defended

A CTD rosette collects and measure ocean water properties at different depths. Photo: UW

the use of the word "hypoxia" when talking about waterborne species while rejecting a uniform definition in terms of concentration.

"Aquatic ecologists have borrowed the term 'hypoxia' (low oxygen) from the medical community, but the meaning and processes are the same," they said in the journal *Biogeosciences*. "The medical condition is where the body is deprived of adequate oxygen. Similarly, a water body can be deprived of adequate oxygen...

"There is no single defined concentration at which marine, coastal or estuarine waters become hypoxic to the resident organisms, nor is there consistency in units of oxygen used to express hypoxia."

The effects of hypoxia—including behavioral, physiological and reproductive—depend on the species, stage of life and history of exposure to low oxygen, the researchers said. Therefore, multiple definitions and differing units of measure are acceptable in the scientific world.

"Most aquatic ecologists and oceanographers would agree that there is no 'conventional' definition of hypoxia and that the relevant thresholds are context-dependent," they contended, adding that hypoxia can be defined for any given study, provided that the information is clearly presented.

Recent studies

A study published in the journal *Nature Climate Change,* focuses on low-oxygen damage to coral reefs around the world, and the 22 authors seem to support the argument for abandoning 2 mg/L as any sort of overall threshold for hypoxia, particularly for coral reefs.

Lethal thresholds for tropical reef organisms can be as high as 4 mg/L, and sublethal thresholds can be even higher, especially in conditions of warmer water, according to the report, which looked at 32 experimental sites on 12 coral reefs around the globe.

For their study, the researchers defined four hypoxia thresholds beginning with "weak hypoxia" at less than or equal to 5 mg/L, which they said would include 90 percent of the sublethal effects observed among bottom-dwelling organisms in temperate waters. The other levels were "mild hypoxia" at or below 4 mg/L, "moderate hypoxia" at or below 3 mg/L, and "severe hypoxia" for the conventional 2 mg/L and below.

"Nearly all reefs in our study (84%) experienced weak hypoxia, while 50%, 34% and 13% experienced mild, moderate and severe hypoxia, respectively, at some point during the data collection period," they said.

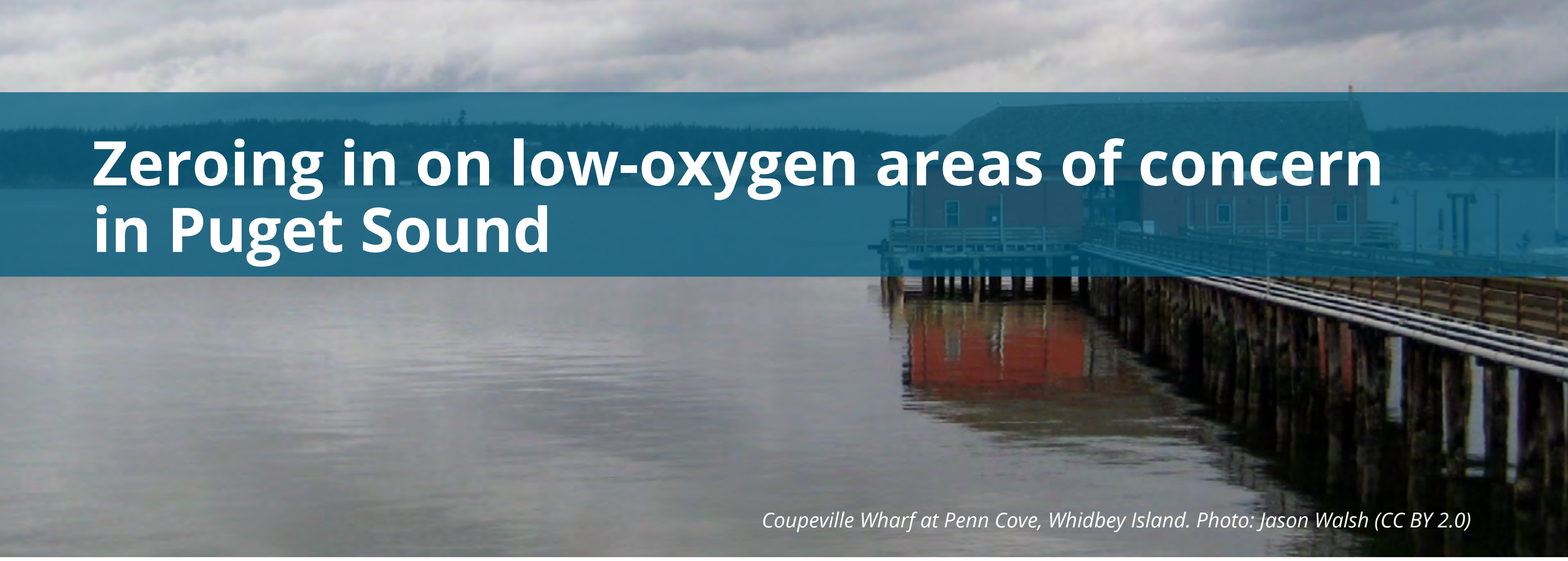
"Notably, oxygen loss and hypoxic events are not occurring in isolation from other stressors," they said. "Oxygen and temperature are tightly linked in terms of organism metabolism and together may severely limit species performance."

Higher temperatures trigger increased respiration among reef species, causing declines in oxygen and increased acidification, all leading to heightened stress and greater risks of mortality for a multitude of species. Climate change is expected to increase the frequency, duration and intensity of hypoxia in all four categories, as more "mild" events cross the threshold into "moderate," and "moderate" events become "severe hypoxia," according to their findings.

The definition of hypoxia may undergo further refinements in the future, but the worldwide challenge remains the same: to improve the marine environment and reduce the effects of low oxygen, hypoxia, or hypoxia. ■

This article first appeared in *Salish Sea Currents Magazine.*

Zeroing in on low-oxygen areas of concern in Puget Sound



Coupeville Wharf at Penn Cove, Whidbey Island. Photo: Jason Walsh (CC BY 2.0)

Low dissolved oxygen levels put aquatic life in Puget Sound at risk— but not everywhere. A combination of careful monitoring efforts and powerful computer models are now enabling scientists to identify which areas of our regional waters are most prone to low oxygen levels, when, and why.

By Sarah DeWeerdt

Takeaways

- Puget Sound experiences low dissolved oxygen particularly in shallow bays and inlets, with levels in Penn Cove dropping as low as 0.18 mg/L in late summer and early fall.
- Washington State's water quality standards set dissolved oxygen levels between 4-7 mg/L (mostly 6-7 mg/L in Puget Sound) or above modeled estimates of natural conditions, whichever is lower; and stipulates that human activities cannot reduce levels by more than 0.2 mg/L or 10%, whichever is less.
- Computer models have identified more than a dozen areas around Puget Sound that may violate oxygen standards due to human activities.
- While only 9% of nitrogen in Puget Sound comes from human activities, this small amount can trigger algal blooms.

LATE ONE AFTERNOON in the middle of March, a gray whale dives in Penn Cove off Whidbey Island. On the right underside of its tail fluke, three large, irregularly shaped pale spots mark this whale as CRC2356 or Stalwart, one of a dozen or so gray whales known as "Sounders" who descend on Puget Sound each spring to feast on ghost shrimp. The whales scoop great mouthfuls of mud from shallow tidal flats and force it out through their baleen plates, gulping down the tasty four-inch crustaceans that remain.

In front of the whale and a little to the west lies the grid of wooden rafts belonging to Penn Cove Shellfish, which at this time of year will be hung with lines coiled at the top of the water to catch mussel spat from the spring spawn. Penn Cove is one of the most productive shellfish-growing locations on the U.S. West Coast, rich in nutrients that fuel the growth of the plankton that mussels and other filter-feeders depend on.

Beneath this idyllic scene, at the bottom of the cove on the seafloor, water trickles into the cove from the Pacific Ocean. The ever-so-faint current might be barely registered by the knobby papillae on the bodies of sea cucumbers that hang out below the rafts and feed on the bonanza of mussel waste that sifts down from above.

The ocean water has traveled along the Strait of Juan de Fuca, through Admiralty Inlet and around the southern tip of Whidbey Island then up through Saratoga Passage, sluicing through glacier-carved channels and tipping headlong over sills to reach Penn Cove. Its arrival will establish how well the local ecosystem "breathes" and whether life can continue to thrive here. This springtime inflow will shape dissolved oxygen (DO) levels in the cove until sometime in the fall.

It is a simple fact that almost all living things need oxygen to survive — from whales to shellfish — and diminished levels of dissolved oxygen can make marine organisms more vulnerable to disease, interfere with their sensory perception, impair their reproduction, and may even be fatal. In Penn Cove, for example, oxygen levels at the bottom of the water can fall as low as 0.18 mg/L in the late summer and early fall.

Among other consequences, low oxygen may [weaken mussels' byssal threads](), which they use to attach themselves to the rocks, ropes, or other substrates on which they live. Although there have been no dramatic consequences of low oxygen in Penn Cove so far, such as fish kills that have occurred in some parts of Puget Sound, scientists are closely monitoring trends in oxygen levels here and elsewhere as the climate warms and pressures from human development continue.

This is why scientists consider dissolved oxygen to be a critical measure of an area's water quality, and it's why a pair of sleek, white, two-foot-long cylinders are attached to a piling on the Coupeville Wharf. The cylinders contain sensors that log water temperature, salinity, pressure, pH, dissolved oxygen, chlorophyll, turbidity, and nitrogen every 15 minutes as part of a King Country program to monitor water quality in the Whidbey Basin of Puget Sound.

The scene at Penn Cove is the backdrop to an effort to understand which parts of Puget Sound suffer from low levels of dissolved oxygen, when, and why. Problems with dissolved oxygen in Puget

Mussel rafts in Penn Cove, Whidbey Island. Photo: Adobe Stock

Sound vary both by location and by season, this research is revealing. But many questions remain – and the answers could have multi-billion-dollar stakes.

Elements of the problem

Penn Cove, like many parts of Puget Sound is naturally prone to low oxygen due to circulation patterns and bathymetry, or the shape of the underwater terrain. The question of what exactly constitutes [natural conditions in Puget Sound] has been contentious. But the broad strokes of oxygen dynamics are well understood. Waters of different temperature or salinity tend not to mix, so fresher, more oxygenated water pouring into Puget Sound from rivers tends to sit on top of saltier, oxygen-poor marine waters from the Pacific Ocean. This phenomenon, known as stratification, worsens the depletion of oxygen in bottom waters. Long, narrow, and shallow bays and inlets are especially prone to this issue because their waters are slow to be exchanged with water from larger water bodies. Penn Cove, which pushes more than three miles into the eastern shore of Whidbey Island like a finger making a deep dimple in soft bread dough, is a typical example.

While some parts of Puget Sound are prone to low oxygen year-round, the problem tends to be worse and more widespread in late summer and fall. This is partly because warm weather during summer makes stratification more pronounced. In addition, summer's long, sunny days drive the growth of photosynthetic organisms including microscopic cyanobacteria and algae. When the blooms die back, the remains of these organisms fall to the bottom and are broken down by bacteria, a process that consumes oxygen.

Human activities can also worsen oxygen depletion, chiefly by increasing the level of nutrients, especially nitrogen, entering Puget Sound. Excess nitrogen comes from agricultural runoff, fossil fuel burning, and especially discharges from wastewater treatment plants serving the region's burgeoning human population.

The large majority of human-caused nutrient pollution comes from wastewater treatment plants, according to Colleen Keltz, Communications Manager for the Water Quality Program at the Washington State Department of Ecology. "[It] doesn't mean they generate the pollution," she says. "It means we, as humans, pee and flush the toilet." When that happens, nitrogen-rich effluent from wastewater treatment plants can act as a fertilizer, turbocharging summer algal blooms and making the subsequent fall in dissolved oxygen more acute.

Most of the nitrogen found in Puget Sound comes from natural sources, the vast majority of that from the ocean. An estimated 9% of the nitrogen can be traced to human activities in Washington State. While the anthropogenic contribution is small overall, nitrogen is normally a limiting nutrient in Puget Sound waters, so just a little extra may result in substantial overgrowth of phytoplankton blooms and subsequent lack of oxygen.

Just how much that amount might tip the balance has become a matter of debate that is driving scientific research and has set off a series of legal battles over what should be done about it.

Areas of concern

Excess human-caused nutrients are [a widespread problem] affecting waterways worldwide. Nutrient reduction strategies have yielded success in cleaning up [the Chesapeake Bay] and waters around [Denmark.] In Puget Sound, some Native tribes and local communities, especially in areas with waters affected by low oxygen, argue that technology to remove nutrients from wastewater should be added to treatment plants around the region. But this strategy could cost billions of dollars, costs that would be passed on to utility ratepayers. And it's important to know exactly where nutrient pollution needs to be reduced and by how much.

Some guidance on that question comes from water quality standards. The Washington State Department of Ecology regulates dissolved oxygen levels in marine waters as part of its responsibility for implementing the federal Clean Water Act. Standards range from 4 to 7 milligrams of oxygen per liter, depending on the needs of the species that live (or could live) in a particular location. For most of Puget Sound this so-called biologically based or numeric standard is 6 or 7 mg/L; in Penn Cove it is 6.

Waters can fall afoul of state dissolved oxygen standards without being hypoxic, a term that [most commonly indicates] dissolved oxygen levels of less than 2 mg/L. But state officials say these higher standards are necessary to protect the health of aquatic life. "These are the oxygen concentrations that we know the fish that are existing in these specific parts of Puget Sound and other critters need to thrive," says Jeremy Reiman, an environmental planner at the Department of Ecology working on water quality standards.

Washington State is currently [in the process of re-establishing] water quality standards based on the dissolved oxygen levels that would have historically, prior to European settlement, prevailed at a

Penn Cove (circled in red), like many parts of Puget Sound is naturally prone to low oxygen due to circulation patterns. Arrows and width of the blue path shown on the map indicate both direction and change in average annual inflow rate of ocean waters for 2017. The ocean inflow rate at the Strait of Juan de Fuca diminishes The volume of ocean water that enters Puget Sound diminishes (indicated by arrow width) as it reaches the end of narrow bays and inlets like Penn Cove taking longer to flush out excess nutrients and pollutants. Map: Puget Sound Institute; Data source: MacCready et al. 2021

particular location. Once such "natural conditions" criteria are in place, they will replace the numeric standard wherever they apply. Under the natural conditions regime, state regulations include an "anthropogenic allowance" for human impacts. Human activities cannot reduce dissolved oxygen by more than 0.2 mg/L or 10% (whichever decrease is smaller)..

A primary tool for understanding the human influence on oxygen levels in Puget Sound is the Salish Sea Model (SSM), a state-of-the-art computer simulation developed by the Pacific Northwest National Laboratory in collaboration with the Washington Department of Ecology. The SSM can also provide a more detailed, high-resolution picture of current oxygen conditions than is available from on-the-water monitoring data – and thus point to areas where greater monitoring efforts are needed.

In one SSM analysis, the model revealed roughly a dozen and a half areas around Puget Sound that may be out of compliance with state dissolved oxygen standards due to human activities and where more information is needed about local oxygen dynamics. The areas of concern include parts of Hood Canal, a long, narrow, deep arm of the sea that has what researchers in [a 2018 paper on hypoxia in Puget Sound] dubbed a "classic fjord-type circulation" with strong stratification and a "nearly stagnant" bottom layer, and regularly becomes depleted of oxygen in the summer. The list also includes many shallow terminal bays and inlets around the region. Some of the places on the list have long been known as areas prone to low oxygen. Budd Inlet, in the far southern reaches of Puget Sound near Olympia, has been the subject of nutrient cleanup efforts since the 1990s. But the list also includes some new areas of concern, including Penn Cove. The analysis provides a focus for concern about low oxygen levels in Puget Sound: the problem isn't everywhere, says Stefano Mazzilli, senior research scientist at the University of Washington Puget Sound Institute who has been working with the model. "There is only a finite number of places," he says, "So we can start by focusing on what's driving change in those places." [Editor's note: The Puget Sound Institute is the parent organization of the Encyclopedia of Puget Sound.]

A tale of two models

More clues about when, where, and why low oxygen levels occur in Puget Sound come from a second computer model, known as LiveOcean. An analysis presented at the Science of Puget Sound Water Quality workshop series in February focused on six inlets in Puget Sound where LiveOcean predicts that average daily oxygen levels at the bottom of the water fall below 2 mg/L —that is, become hypoxic —during the late summer and early fall. That list includes Penn Cove.

Researchers analyzed these six hypoxic inlets compared to seven better-oxygenated inlets in Puget Sound to understand what processes contribute most to the development of low oxygen levels during August and September. According to the prevailing model of coastal oxygen dynamics, hypoxia might develop in a particular area because the water there starts out with relatively low oxygen levels, that is, at the beginning of the growing season in spring; because biological processes such as the breakdown of phytoplankton blooms deplete oxygen quickly; or because water sticks around in the area for a long time before being replaced with more oxygenated water from elsewhere.

The first and third of those factors are the main determinants of susceptibility to hypoxia in Puget Sound's inlets, the analysis showed. "The most hypoxic inlets in Puget Sound are not ones that act as isolated hotspots of high DO consumption or high DO depletion rates," Aurora Leeson, a graduate student in the laboratory of University of Washington oceanographer Parker MacCready, which developed and maintains LiveOcean, told the workshop. "Instead, deep DO concentrations in terminal inlets of Puget Sound are strongly influenced by what flows into the inlets and how long it takes to flush the inlet."

This analysis is based on 2017 data and represents current conditions, Leeson says. A next step is to analyze a reference scenario without anthropogenic nutrient inputs, then compare the two to determine how wastewater treatment plants and other human activities may be contributing to the dynamics that produce hypoxia in these inlets.

The two models have many differences: SSM divides Puget Sound into a landscape of triangles, while LiveOcean uses a grid of squares; SSM offers greater resolution at the surface of the water while LiveOcean divides the depth of the water column into finer layers; SSM focuses on minimum oxygen concentrations to LiveOcean's tidally-averaged daily values; and so on.

But while some details of the analyses conducted and results obtained may differ, in broad strokes the two models paint a similar picture of the problem of hypoxia in Puget Sound: The areas most affected are Hood Canal and many shallow bays and inlets with long flushing times. But the causes of hypoxia can't be localized just to those affected areas; "Puget Sound is so interconnected," Leeson told *Salish Sea Currents*.

An algal bloom in Hood Canal on August 21, 2022 turns the water bright turquoise and can be seen from space. Photo: NASA Operational Land Imager-2 on Landsat 9

This means it's necessary to reduce nutrient inputs not just near hypoxia hotspots but throughout Puget Sound, says Ecology's Colleen Keltz. The agency has sought to incorporate these insights into regulations with its Puget Sound Nutrient General Permit, issued in December 2021 and covering 58 wastewater treatment plants that discharge into different parts of Puget Sound.

But on February 28, the Washington State Pollution Control Hearings Board struck down this approach, ruling that the general permit cannot be a mandatory overlay on existing individual permits. Ecology decided not to appeal the ruling and is shifting to a voluntary general permit approach.

Trends and tinkering

Meanwhile, efforts continue to both refine the models and build a better understanding of actual conditions in the water. Shallow terminal embayments – precisely the sorts of areas that are prone to low oxygen levels – are also difficult to render precisely in large-scale ocean models, says Taylor Martin, an oceanographer with King County.

Spurred by SSM results suggesting that nutrient discharges from King County wastewater treatment plants could contribute to low oxygen levels in Penn Cove and nearby areas, the county has launched a water quality monitoring program in the Whidbey Basin. "A lot of the water that comes from King County flows back North," Martin explains. "A lot of it goes back out Admiralty Inlet. But not all of it. Some of it does slosh around to the East side of Whidbey."

King County began sampling water quality at 10 locations in Whidbey Basin in 2022, initially collecting data twice and now once monthly. In 2023 they installed continuous monitoring instruments at three locations – near Port Susan, near the mouth of Penn Cove, and at Coupeville Wharf – that record data every 15 minutes.

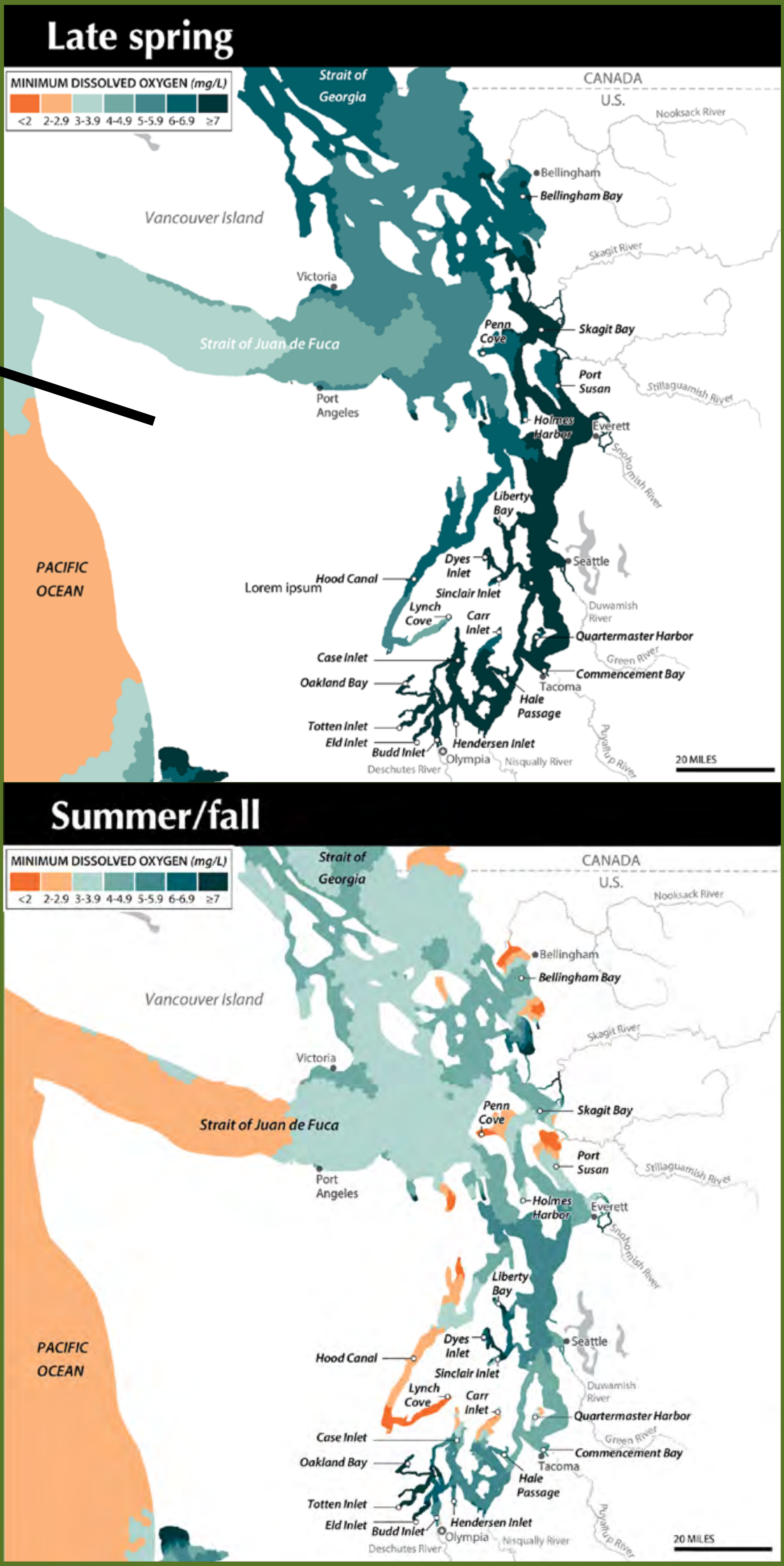
So far in Penn Cove, "I think we've seen basically exactly what we expected to see," Martin reports. "Dissolved oxygen does get quite low in the late summer and fall." The county plans to continue monitoring these areas to see if there are any trends in the timing or duration of hypoxia – which can be difficult to establish because patterns of dissolved oxygen can vary so much from year to year, Martin says.

The Department of Ecology has been continuing to tinker with the SSM to find the best strategies for nutrient reduction, looking for scenarios in which the model predicts the highest compliance with dissolved oxygen standards throughout Puget Sound. Its modeling team teased the latest results at a meeting of the Puget Sound Nutrient Forum on March 27, and the agency plans to release the results along with an Advance Restoration Plan to reduce nutrients in Puget Sound in June. ■

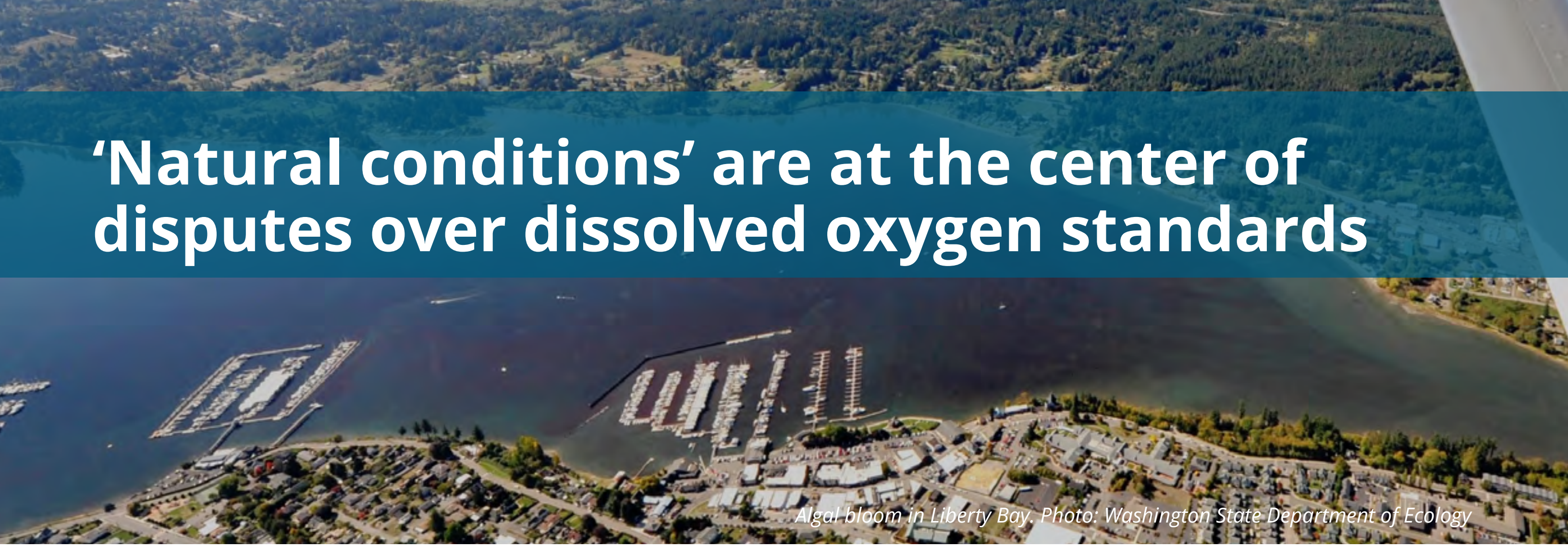
This article first appeared in *Salish Sea Currents Magazine.*

Areas of concern

Low dissolved oxygen occurs naturally in the ocean and in Puget Sound, particularly where circulation is poor, including deep waters, and some bays and inlets. Areas of concern typically manifest in late summer or early fall.



Hood Canal and the 19 bays and inlets marked with pointer lines on these maps represent areas where models (based on state regulations) predict that human activities could further reduce dissolved oxygen levels. Maps: PSI; Data source: Salish Sea Model for the year 2014.



‘Natural conditions’ are at the center of disputes over dissolved oxygen standards

Algal bloom in Liberty Bay. Photo: Washington State Department of Ecology

Oxygen is indisputably essential to aquatic life, but conflicts are brewing over water quality standards mandated in state regulations. By some estimates, those definitions could affect billions of dollars in state and local spending.

By Christopher Dunagan

Takeaways

- Washington Department of Ecology aims to establish “natural conditions” standards since some of Puget Sound’s waters have never met current numeric oxygen criteria, even in prehistoric times.
- Laboratory studies of species’ oxygen requirements may not reflect real-world conditions where fish can acclimate to lower oxygen levels or move to better waters.
- Ecology’s proposed solution allows for computer modeling to determine prehistoric oxygen levels plus a small allowance (0.2 mg/L or 10%) for human impacts.
- Billions of dollars may be needed to upgrade sewage treatment plants to meet oxygen requirements. These costs would be passed to customers through higher sewer rates.

BEFORE early settlers built the region’s first sawmill at Tumwater in 1848, before Arthur Denny and his party settled the future city of Seattle in 1851, and before the federal government created Washington Territory in 1853, the waters of Puget Sound and its freshwater streams were as clean as nature could provide. Fish and wildlife were abundant, having adapted to local conditions alongside native people of the area.

Needless to say, things have changed since those days. In the parlance of today’s water-quality regulations, the clean waters of yesteryear are known as “natural conditions.” Nobody believes that we will ever see those conditions again, but the term “natural conditions” has taken on a profound meaning as a point of reference. How far do we humans want to go in restoring polluted waters and limiting unhealthy discharges of wastewater into Puget Sound?

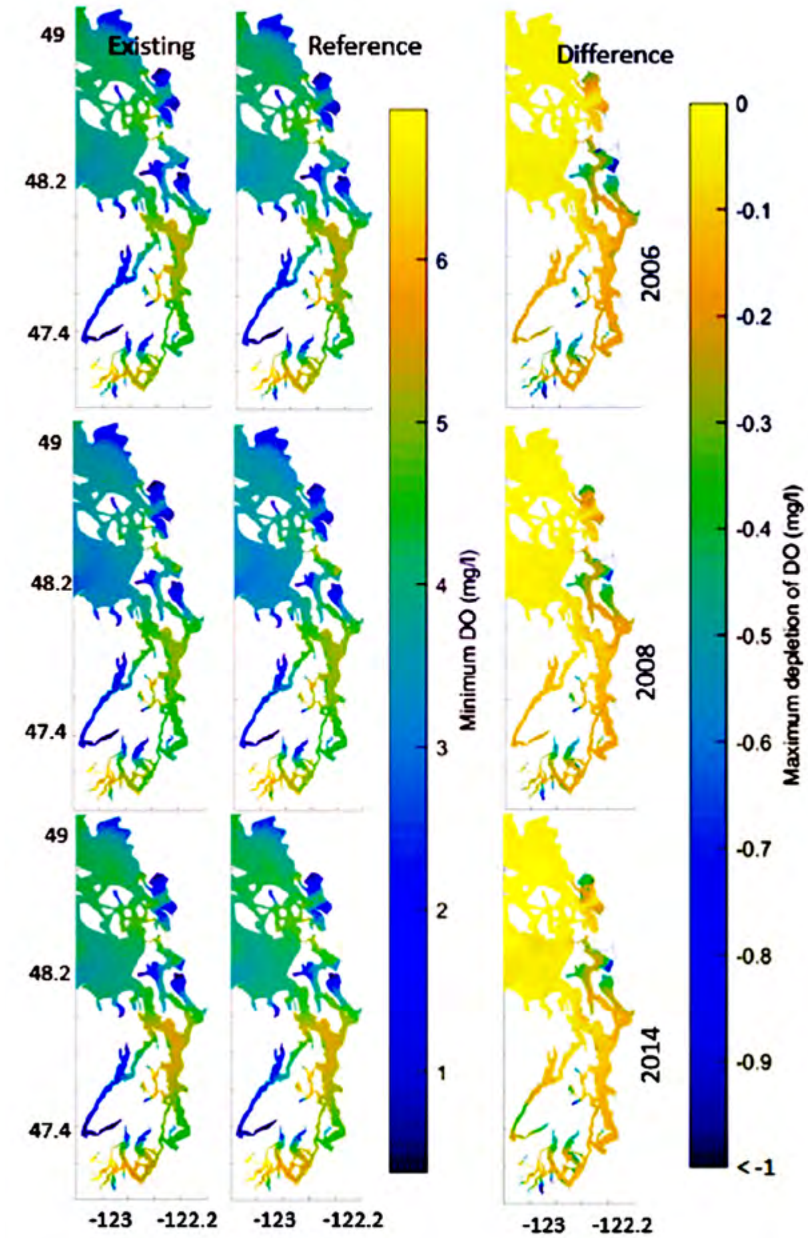
Washington Department of Ecology is currently struggling to establish a regulatory system involving natural conditions, based on the idea that it makes no sense to set cleanup goals beyond the best that nature has ever provided. The federal Environmental Protection Agency, which maintains ultimate authority over the nation’s waterways, overturned Ecology’s existing natural conditions rule in 2021. Since then, Ecology has been working on a revision, particularly addressing water-quality goals for temperature and dissolved oxygen.

The agency recently completed limited rules for setting cleanup standards in defined locations. The ongoing effort is to create an enduring “performance-based” program that would empower experts to identify natural conditions anywhere in Puget Sound, along with an approved allowance for human degradation. The first draft received rather harsh comments from the EPA. A revised proposal that addresses only dissolved oxygen for marine waters was released for public comment in March 2025.

> **Documentation used to justify dissolved oxygen standards, developed more than 50 years ago, appear to be lost, according to Ecology’s Water Quality Program, but agency officials maintain that available studies still support those numeric limits as protective of aquatic creatures.**

In a letter to Ecology about the first draft, Rebecca Garnett, manager of standards and assessment for EPA’s Region 10, said any new water quality criteria must meet scientific standards, be spelled out in sufficient detail, and fully protect aquatic creatures. “As currently proposed,” she wrote, “the EPA is concerned that Ecology’s performance-based approach for developing site-specific natural conditions criteria is not sufficiently ‘binding, clear, predictable, and transparent.’”

In a legal sense, water quality standards are essential, because they determine how much money is spent by government and industry to clean up our troubled waterways and improve survival for fish, crabs and other animals. According to some estimates, billions of dollars may be needed to bring major sewage-treatment plants into compliance.



The minimum dissolved oxygen level for most of Puget Sound is 7 mg/L, and 6 mg/L for areas to the west of Whidbey Island and into Bellingham Bay. The natural or "reference" condition map (center) shows that few areas of Puget Sound meet these minimum numeric standards. Areas in the difference map (right) that are green to blue are most sensitive to depletion of dissolved oxygen from human sources. Map: Washington Department of Ecology

Documentation used to justify dissolved oxygen standards, developed more than 50 years ago, appear to be lost, according to Ecology's Water Quality Program, but agency officials maintain that available studies still support those numeric limits as protective of aquatic creatures.

Developing these new water-quality standards is complicated and intriguing, involving computer models to describe water-quality conditions that existed long before people changed the environment. A typical method of estimating natural conditions is to go out and measure current conditions in specific areas and then subtract all known causes of human degradation, often with the help of computers.

Natural conditions criteria may come into play when a body of water fails to meet established "numeric criteria." Numeric criteria are levels of oxygen and temperature that scientists say will meet the biological needs of aquatic creatures. Exceptions to numeric criteria are allowed for areas that have naturally lower levels of oxygen or naturally higher temperatures than the numeric criteria. For oxygen, the numeric criteria for most of Puget Sound is no less than 6 or 7 milligrams per liter, depending on the location. Based on studies, it appears that most of Puget Sound has never met those standards — not even in prehistoric times. This means that we could eliminate all human causes of low oxygen and still come up short of the approved numeric criteria.

This dilemma raises the stakes for choosing the correct natural conditions criteria. It also raises questions about whether Puget Sound is using the correct numeric standards, originally developed in 1967. Some officials in local government and industry as well as some scientists are calling for Ecology to overhaul the numeric criteria for oxygen throughout Puget Sound. The nonprofit advocacy group Association of Washington Cities, among others, would like the Legislature to fund a study to determine the actual needs of aquatic creatures in Puget Sound. For now, Ecology has placed a higher priority on developing natural conditions criteria.

"This matters," states a news release from the agency, "because Ecology and all organizations working on clean water efforts need to focus the state's pollution-reduction efforts on waterbodies where humans are causing pollution, not on waterbodies that are naturally different."

Fitting nature into a regulatory framework

The Clean Water Act of 1972 provides the regulatory foundation for cleaning up Puget Sound, establishing a national policy to "restore and maintain the chemical, physical and biological integrity of the nation's waters." The Department of Ecology, authorized by the EPA to administer this law in Washington state, develops water quality standards designed to protect aquatic species (particularly the most sensitive ones), human health, activities, and even aesthetics.

Oxygen is considered an essential element for sea life in marine waters. Numeric criteria for oxygen in Puget Sound, ranging from 4 to 7 milligrams per liter, date back to 1967 under the Federal Water Pollution Control Act, the predecessor to the Clean Water Act.

Most of Puget Sound is designated for a minimum of 7 mg/L. Areas to the west of Whidbey Island and into Bellingham Bay are designated for no less than 6 mg/L. The innermost portions of Tacoma's Commencement Bay, Olympia's Budd Inlet and Shelton's Oakland Bay are designated for 5 mg/L, down to 4 mg/L in a few relatively tiny areas of those waterways.

Critics argue that 6 or 7 mg/L is generally overly protective of water quality, since most areas of Puget Sound apparently never met those standards, not even in prehistoric times when marine species were abundant. Some say the criteria should be updated with more recent science, perhaps considering the depth of channels and other factors that affect natural oxygen levels. Chesapeake Bay on the East Coast has taken this approach. As things stand, the numeric criteria for Puget Sound are destined to be largely displaced by natural conditions criteria based on computer models.

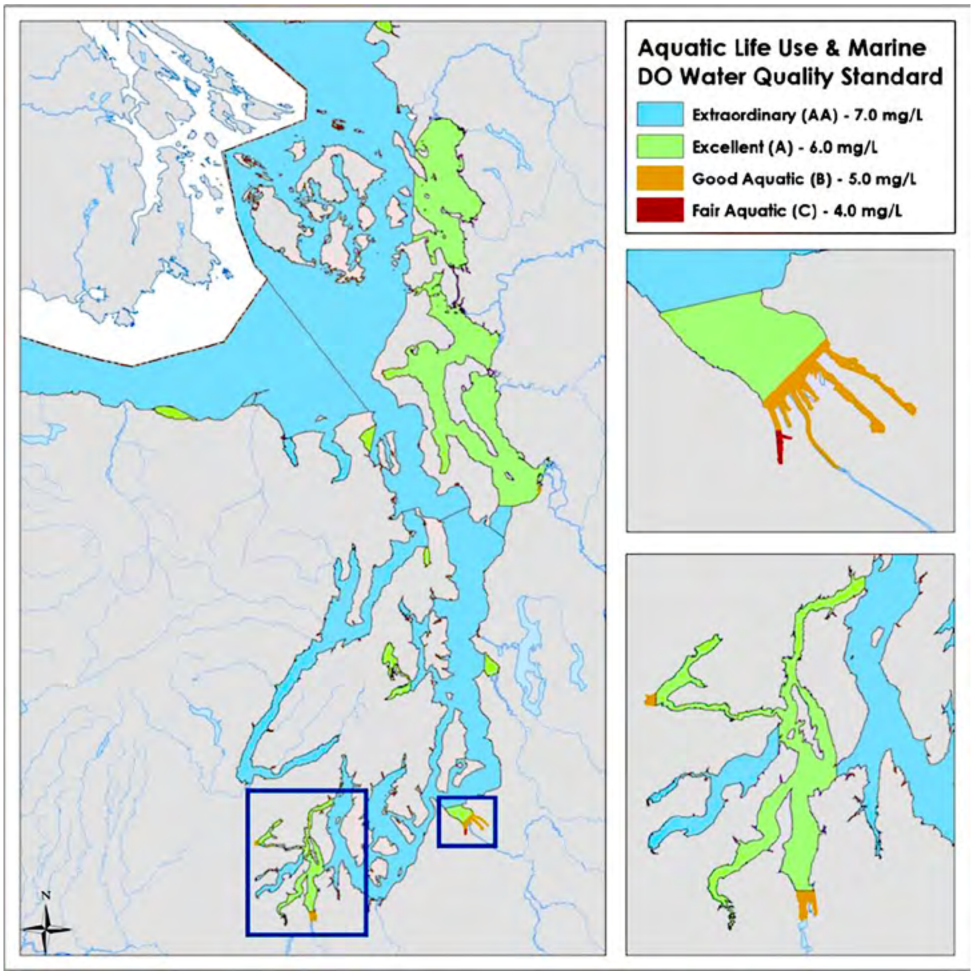
Biological needs of species

The concept of using a numeric standard for water quality is rather simple, perhaps too simple, some people say. For example, one can estimate, based on laboratory studies, the biological needs of salmon, including healthy levels of temperature and oxygen. These biological requirements may vary, depending on the activity of the fish, its body condition and other factors.

The biological needs may be complex and dynamic, yet Washington's numeric water quality criteria are reduced to single numbers. Much of Puget Sound has been designated as "extraordinary" water quality, a category that calls for a minimum oxygen level of 7 mg/L and a maximum temperature of 13 degrees C (55.4 F). Other criteria establish limits for turbidity, acidity and bacteria. Besides "extraordinary," various areas of Puget Sound have been designated as "excellent," "good" or "fair," each with their own criteria to protect named species residing there.

Oxygen and temperatures can vary by location and depth in Puget Sound. State regulations call for taking measurements at depths that represent the "dominant aquatic habitat" at each monitoring site. Such monitoring helps to determine whether a water body complies with established criteria or is "impaired" for certain water quality parameters. Because conditions change over time, particularly with seasonal cycles, some areas may comply at one time but not another.

Since few areas of Puget Sound can meet the numeric criteria for dissolved oxygen at all times, even under natural conditions, some individuals and groups are calling



According to water quality standards for Puget Sound, as shown on the map, most of the waterway should contain at least 7 milligrams per liter of dissolved oxygen to meet numeric criteria. Where natural levels of oxygen are believed to be lower than these numeric criteria, the Washington Department of Ecology would allow for "natural conditions criteria." The agency has proposed a revised process for determining natural conditions. Map: Ecology

for revisions to the criteria. They contend that limits of 6 or 7 mg/L are considerably higher than needed to protect marine life in Puget Sound. Rather than resorting to computer models to determine natural conditions criteria, scientific studies could help establish new numeric criteria based on biological needs.

"Ecology has acknowledged that it has no documentation as to the scientific basis for the marine DO standards that were adopted by a predecessor agency in 1967," said Carl Schroeder of the Association of Washington Cities, commenting on the proposed natural conditions criteria.

Schroeder noted that cities are responsible for many of the sewage-treatment plants in Puget Sound, including those facing costly upgrades to improve oxygen conditions. Since costs must be passed on to customers via higher sewer rates, local governments must be able to explain the rationale for Ecology's water quality standards, he said.

After 56 years without a clear scientific foundation, he continued, "it is startling that Ecology continues to move forward without seeking or incorporating information on the dissolved oxygen needs of the organisms present in Puget Sound."

During last year's legislative session, Schroeder and others attempted to get Washington lawmakers to appropriate $500,000 for a scientific review of the biological needs of Puget Sound species in connection with the state's cleanup standards. The proposed study would have involved the Washington Academy of Sciences. Funding for the study was approved by the House but failed to survive final negotiations in the Senate. This year, Schroeder continues to push for legislative funding, despite tight budget conditions.

Lincoln Loehr, a retired oceanographer and environmental consultant, has been on a crusade of sorts to get Ecology to review the numeric criteria for oxygen. He first petitioned the agency to review the oxygen criteria in 1998, before most people were aware that natural conditions criteria would become such a key factor in setting cleanup targets. Loehr shared his views with many technical groups working on the low-oxygen problems of Puget Sound, and in 2017 he petitioned Ecology again to review the numeric criteria.

Loehr wrote, "While the state can identify waters as not meeting these criteria, that determination does not demonstrate that the waters are impaired, as the comparison is made with baseless criteria. Similarly, computer modeling to compare to a 0.2 mg/L decrease in DO from human causes (part of the state's criteria) is not a basis for demonstrating impairment, as it has no biological basis."

Responses from EPA officials have offered no support for revising the state's numeric criteria, which federal law says can be more restrictive than federal requirements. Ecology officials defend the existing criteria as being protective of marine species, but critics contend they are overly protective. Loehr argues in favor of changes to the numeric criteria, saying the Clean Water Act calls for standards that accurately reflect the "latest scientific knowledge."

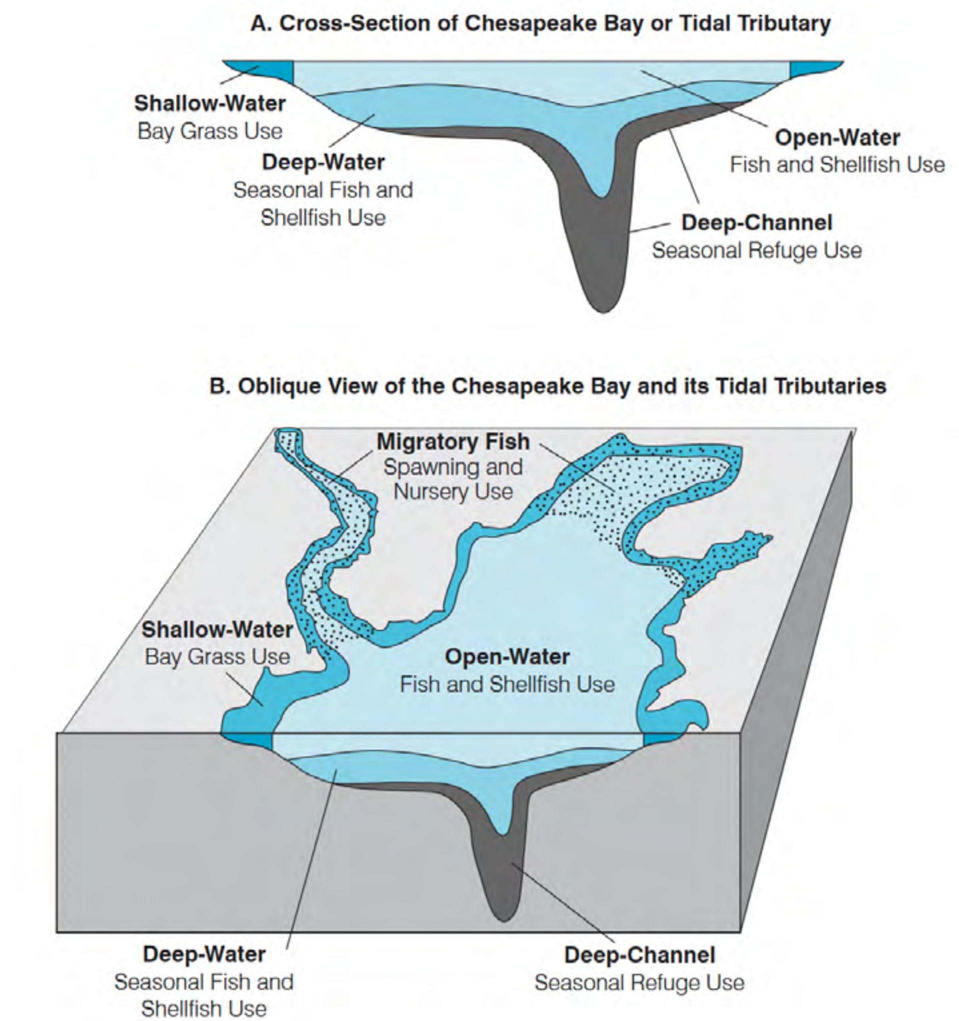
Sara Thitipraserth, director of natural resources for the Stillaguamish Tribe, expressed similar concerns in letters to Ecology and the EPA.

"It is the view of the Stillaguamish Tribe that the Marine Dissolved Oxygen Water Quality Criteria of Washington state are in need of thoughtful, science-based revision," she wrote. "They are outdated, simplistic, and fail to consider the geography and hydrology of Puget Sound. Neither are they based on or referenced with scientific research.

Measuring the needs for oxygen

Tim Essington, a fisheries ecologist at the University of Washington who studies oxygen depletion in Puget Sound species, highlights the gap between laboratory measurements and real-world conditions. His research examines "critical thresholds"—the oxygen levels at which fish must make physiological or behavioral changes to survive.

"In the lab, you are measuring routine behavior; the fish is not trying to chase down food," Essington explained. "But in terms of ecological relevance, animals do need to eat. The process of finding food costs oxygen, and there is also the need to avoid predators."



Five habitats types designated for Chesapeake Bay. Illustration: EPA

Fish in natural settings can both acclimate to low-oxygen conditions (like athletes training at high altitude) and adapt over generations. Essington notes that studying species presence in various oxygen conditions can provide insights, though the most sensitive species may have already disappeared from low-oxygen areas—a factor that must be considered when determining appropriate standards.

In Chesapeake Bay on the East Coast, the EPA faced the challenge of low-oxygen conditions by dividing the bay into five habitat types, including considerations for the depth of the water. Since deeper water typically contains less oxygen, dominant species are more tolerant of those conditions. The resulting guidelines (PDF) were completed in 2003 with numeric criteria for oxygen, water clarity and chlorophyll. They were subsequently adopted into regulations by the four governmental jurisdictions around the bay: Washington, D.C. and the states of Maryland, Virginia and Delaware.

Proponents of changing Washington state's numeric criteria for oxygen often point to Chesapeake Bay as an example of how to fit biological needs into a regulatory framework.

EPA identified and described five habitats to ensure the protection of the living resources of the Chesapeake Bay and its tidal tributaries. Some say a similar approach would be appropriate for Puget Sound.

Natural conditions approach

From the beginning, Ecology officials realized that some areas of Puget Sound contained naturally low levels of oxygen that could never meet the numeric criteria, even under the best conditions.

"We have long acknowledged that (portions of) Puget Sound is naturally impaired for DO," said Leanne Weiss, unit supervisor in Ecology's Water Quality Management Division, "and that's why these other processes and options are so important."

In fact, when considering all the nation's waterways, EPA recognized as early as 1997 that natural conditions, absent human impacts, might be lower in oxygen or higher in temperature than numeric criteria in some areas. A 1997 memo (PDF) establishes a policy allowing for numeric limits to be supplanted by natural levels.

Current revisions to Ecology's natural conditions regulations came about from a lawsuit filed by Northwest Environmental Advocates. In response to the lawsuit, the EPA agreed to reconsider its 2008 approval of Ecology's natural conditions rule. After review, the EPA reversed its approval (PDF), leaving Washington without a natural-conditions option for cleanup goals.

One reason for the reversal was the lack of a clear statement that the natural conditions criteria applied only to aquatic life, not to human health standards, according to the EPA. As described in the 1997 EPA memo on natural conditions criteria, aquatic species may adapt over time to waters with naturally low levels of oxygen or high temperature, but that's not the case for humans. People should be protected from harmful natural conditions by changing the "designated use" of a waterway, the memo says. That might mean excluding fishing or other recreational activities or even issuing public-health warnings.

Ecology's revised rule is written to limit its application to aquatic species.

"Having a standard to determine what is normal and natural for a particular waterbody is important information for setting discharge limits and knowing when action is needed to protect or restore water quality," Ecology states on its rule-making webpage. "Nearly every state and many tribal nations have a provision in their EPA-approved water quality standards to protect aquatic life based on natural conditions of the water bodies."

EPA specifically overturned Ecology's natural conditions criteria for both oxygen and temperature in marine waters and freshwater streams. It did not overturn the criteria in lakes, which EPA determined to be adequately protective as written into the rule.

Oxygen is often the driving factor for marine creatures, and it has received much attention from Ecology because low-oxygen conditions are creating serious problems in Puget Sound. While oxygen levels are a concern in some streams, temperature can be a critical factor for fish where logging has removed large trees that help keep the waters cool (Encyclopedia of Puget Sound).

As with oxygen, when studies show that natural conditions are warmer than designated temperatures, streams have been allowed to reach their estimated "natural" temperatures plus 0.3 degrees—the "human use allowance."

EPA did not determine whether the human use allowance of 0.2 mg/L for oxygen and 0.3 degrees C for temperature was or was not close enough to the actual levels expected under natural conditions, but the agency did insist that Ecology provide scientific justification for those allowances. EPA's 1997 memo allowing for natural conditions does not mention any such allowance.

To reinstate natural conditions criteria, Ecology is developing a performance-based approach that would allow for establishment of site-specific temperature or oxygen limits based on computer modeling. Once approved by both Ecology and the EPA, this process would create legally accepted natural conditions criteria without requiring further approval for each implementation.

The proposal maintains the previously established allowable deviations (0.2 mg/L for oxygen and 0.3 degrees C for temperature) from natural conditions. However, Ecology has added one significant change: when natural oxygen levels are already very low (below 2 mg/l), human impacts would be limited to just 10% of the natural level.

Endangered species protections

During the 2008 approval of the natural conditions criteria, federal agencies responsible for protecting listed species under the Endangered Species Act analyzed the effects of Ecology's revised water quality standards for oxygen and temperature, including the relevant human use allowances: 0.2 mg/L for oxygen and 0.3 degrees C for temperature. While the standards may not fully protect listed salmon during all life stages, they are "not likely to jeopardize the continued existence" of the listed species, according to the National Marine Fisheries Service. When the current revisions are complete, the federal agencies are expected to undertake a new analysis of the natural conditions rule, taking into account changing conditions and new research. They must show that the new rule is protective of threatened and endangered species before it can become effective.

Because the performance-based approach relies on computer modeling to identify natural conditions, the process outlined by Ecology prescribes model selection, assumptions, operation and reliability; choice of data; considerations of climate change; interpretation of model outcomes; documentation; peer review; and many other issues. Ecology's proposed revisions have been drafted with guidance from EPA's natural conditions "framework" (PDF).

When first released for public comment, the EPA expressed concerns about the process, calling for "critical steps" to be added and stronger language to ensure the process is "binding" rather than voluntary. A major challenge in this approach is accurately identifying all human sources affecting a waterway, as missed sources could lead to cleanup standards that fail to adequately protect aquatic species.

While an approved performance-based approach would allow Ecology to establish water quality goals without further rulemaking, another approach is to study a particular area and propose water quality criteria that meets the needs of species in that area. Results from this "site-specific approach" would be proposed and adopted as a rule by Ecology with final approval from the EPA.

In the end, whether cleanup goals are based on numeric criteria or on natural conditions, the ultimate goal is to restore water quality for all species in Puget Sound — including, as much as possible, those species that thrived when natural conditions prevailed. ■

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Central Kitsap wastewater treatment plant. Photo: Washington State Department of Ecology

How will nutrient upgrades impact household affordability?

Wastewater treatment plants release about 7% of the nitrogen flowing into Puget Sound. Regulators are proposing new standards that will require major upgrades to these plants to reduce the amount of nitrogen released. If that happens, low-income residents may need special help making their payments.

A 2022 study by the Puget Sound Institute reveals that low-income households face significant financial hardship from rising wastewater bills. While median-income households in the Puget Sound region typically spend less than 2% of their income on sewer bills, the lowest 20% of earners pay an average of 4.4%, with some paying up to 10% of their income.

The study examined current sewer bills for 80 utilities in the region, finding monthly costs ranging from $27 to $161. These costs could increase to between $44 and $196 due to proposed wastewater treatment plant upgrades aimed at reducing nitrogen pollution in Puget Sound. Excess nitrogen can cause algal blooms and oxygen depletion in water bodies.

If implemented, these upgrades could push costs for lower-income households to between 5.4% and 6.5% of their total income, reaching "severe hardship" levels according to Washington state guidelines. Even median-income households would face "moderate hardship" with costs exceeding 2% of income.

In comparison, most U.S. households spent an average of 10.3% of their disposable income on food, according to the US Economic Research Service, a division of the US Department of Agriculture.

"What we found was that sewer bills take up a surprisingly large portion of household budgets for about 20% of the households in the region," said Aimee Kinney, a researcher at the Puget Sound Institute and one of the leaders of the study.

Approaches to address this issue include increased federal and state funding, revised qualification criteria for hardship grants and loans, and a regional low-income assistance program targeting the most vulnerable households.

Read PSI's blog post about the study.

Ecology estimated that nutrient upgrades at wastewater treatment plants will cost the region $1.4 - $5.9B, which represents an additional $17 - $36/month for households (Tetra Tech 2011). The Puget Sound Wastewater Service Affordability Analysis used a standard usage volume (5.5 centum cubic feet/household) escalated Ecology's cost estimates to 2022 dollars and found:

CURRENT RATES

Affordability concerns for the lowest-earning 20% of households

$27 - $161 per month

4 utilities with hardship

1.6%-10.5% of income for the lowest 20% of earners

NUTRIENT ADJUSTED RATES

Affordability concerns for households earning the lowest **and** median income.

$44 - $196 per month

7-17 utilities with hardship

2.1%-13.1% of income for the lowest 20% of earners

The average household spends 10.3% of their disposable income on food nationally.

Estimates are conservatively low

1. Estimates do not account for other upgrades like replacing aging infrastructure and associated sewer rate increases.
2. More recent estimates show nitrogen treatment costs will be significantly more than estimated in Ecology's 2011 report. For instance, Tacoma's upgrades alone could cost around $2 B to achieve 3 mg/L seasonally, which is less stringent than the most recent regulatory limits under consideration.

4

Future considerations

As scientists and policymakers analyze future concerns over low dissolved oxygen in Puget Sound, many questions still remain. Given ongoing impacts from climate change and an ever-growing human population, we know that the water quality of the ecosystem is going to be affected, but by how much and where? This section includes detailed looks at the inevitable concerns posed by global warming. Remarkably, warming temperatures account for roughly half of the dissolved oxygen decline documented in central Puget Sound over the past century. The conditions create a double threat as warmer waters hold less oxygen while increasing marine species' oxygen demands.

Warmer waters will mean less oxygen for species

Photo: John Turnbull (CC BY-NC-SA 2.0)

In time, lower dissolved oxygen worsened by climate change could increase the abundance of rare species in Puget Sound while putting populations of more common species at risk. This article explores how warmer waters will gradually make it harder for many sea creatures to breathe.

By Christopher Dunagan

Takeaways

- Climate change creates a double threat as warmer waters hold less oxygen while increasing marine species' oxygen demands.
- Current warming trends mirror the "Great Dying" extinction event from 252 million years ago, potentially reaching 20% of those conditions globally by 2100 if emissions continue unchecked.
- Marine heat waves like "the blob" cause sudden ecological disruptions beyond gradual warming, with at least four more such events predicted this century threatening North Pacific fish populations.

CLIMATE studies have shown that areas of the world with historically low oxygen conditions are growing in size. At the same time, new low-oxygen areas are being formed. One study estimates that the total volume of deadly low-oxygen waters has quadrupled since 1960.

As climate change results in warmer waters containing less oxygen, Puget Sound could expect to see an increase in species that can live in lower-oxygen waters but a decrease in species sensitive to the warmer conditions. Some species are likely to disappear if trends continue on their current path, according to climate researchers, but much depends on the amount of greenhouse gas emissions in the coming years.

Figuring out how various species will fare under differing conditions throughout the world has been the focus of intense research by Justin Penn, who completed his doctoral degree in oceanography from the University of Washington in 2020. One of Penn's major findings, published last year in the journal *Science,* is his prediction that sea life abundance and distribution will begin to change dramatically by the end of the century if greenhouse gas emissions are not curbed soon.

Tropical waters would experience the greatest loss of diversity over time, according to his findings, while species living close to the poles would face potential extinction.

Underlying Penn's work on climate change is an understanding that most marine animals increase their respiration rates and their demand for oxygen at higher temperatures. Since warmer waters hold less oxygen, climate change produces a double-whammy for creatures trying to survive under warming conditions.

Penn's graduate school adviser, Curtis Deutsch, has spent years studying the interrelated effects of oxygen and temperature. He developed a "metabolic index" to describe the combined temperature and oxygen requirements of a species and to compare those needs with environmental conditions in various places. Deutsch, a former UW oceanography professor, is now affiliated with Princeton University in New Jersey, where Penn is completing his post-doctoral research.

A study published in 2020 by Deutsch, Penn and Brad Seibel of the University of South Florida suggests that a wide variety of marine creatures — from vertebrates to crustaceans to mollusks — already occupy, to varying extents, all the areas that meet their "breathability" needs, described by their metabolic threshold.

Penn combined the metabolic index for various species with predictions of temperature and oxygen from climate-change models. His maps show how the animals might fare in a warming climate. For example, species living in the warm tropics appear to have traits that allow them to better cope with the warming waters compared to those in more temperate areas. But some tropical species are likely to shift their populations toward the poles to find cooler waters with more oxygen.

At the equator, warm, low-oxygen water already constrains the number of species compared to the middle latitudes between the tropical and polar regions. Further warming in the equatorial region would tend to reduce species diversity even more.

At the same time, some species living near the poles might not be able to meet their oxygen demands in the warmer waters of the future. Since they are already in the coolest water on Earth, they would have nowhere to go in a search of cooler water. If unable to adapt, their risk of extinction would be high.

Ancient climate clues to future

Projections of ongoing climate effects on marine life — assuming an accelerating rate of warming — turn out to be not so different from events that took place some 252 million years ago during the "Great Dying," according to a 2018 study by Penn and Deutsch along with fellow researchers at Stanford University.

At the end of the Earth's Permian Period, up to 96 percent of all marine species and 70 percent of all terrestrial species went extinct. It was a time of massive volcanic activity that raised the temperature of the air and water. Researchers have long debated the cause of the mass die-off, speculating about ocean acidity, metal and sulfide poisoning, lack of oxygen and straight-on higher temperatures.

Using models of ancient ocean conditions along with estimates of metabolic demands by prehistoric creatures, Penn was able to show that the physiological stresses caused by ocean warming and the accompanying loss of oxygen could account for more than half of the losses in marine species during the Great Dying.

The pattern of loss — more toward the poles — is predicted by computer models used in the study and confirmed in the fossil record, which reveals a before-and-after picture of species found in the ocean.

The pattern is similar to what he has predicted for today's world. Assuming current trends in emissions, ocean warming would reach 20 percent of that in the late Permian by the year 2100 and between 35 and 50 percent by 2300, according to Penn. Based on his analysis, if things don't change, it is quite possible that the Earth will experience another mass extinction, based on human actions instead of volcanic activity.

The metabolic index may be helpful in identifying habitats with enough oxygen for certain species to survive. But it does not describe current population distributions, how populations may shift in response to warming, nor how quickly

Jellyfish can survive in low-oxygen conditions. Photo: Haila Schultz/University of Washington

one species may replace another based on their tolerance for low-oxygen conditions. Some researchers have speculated that a reported increase in jellyfish in Hood Canal may be attributed in part to their ability to survive in low-oxygen waters and out-compete less tolerant fish, such as herring.

Which species will dominate?

Because of the complex nature of food webs, it is hard to predict winners and losers, said oceanographer Evan Howard, a UW graduate who now works for Curtis Deutsch at Princeton. According to Howard, a particular but important challenge is to understand primary productivity at the base of the food web. Despite robust predictions of future temperature and oxygen, he said unknown factors make it difficult to describe the type and extent of future phytoplankton growth. Ultimately, phytoplankton are a key to future conditions affecting growth, reproduction, competition and predation for much of the food web.

Upwelling of ocean waters along the West Coast brings nutrient-rich waters from the depths, increasing plankton growth and boosting natural production. The rate of upwelling is driven by natural oceanic cycles influenced by the added and increasing effects of climate change.

"We have this teeter-totter of natural climate variability that sometimes gets outside of the norm and into conditions that we have never seen before," Howard said.

His studies of anchovies and oxygen conditions along the West Coast led him to predict a complete loss of anchovy habitat in the southern part of their range by the end of this century. That would include waters off the Mexican coast reaching into Southern California.

During warm-water "heat waves," such as the so-called "blob" from 2014 to 2016, a greater number of anchovies were observed in Puget Sound, but the cause is not well understood. Howard wonders how much those observations were the result of migration of anchovies into Puget Sound from other areas versus a movement of fish from deeper to shallower waters to get more oxygen.

"Sometimes you see an abundance in animals in one place because they are stressed somewhere else," he said, noting that the overall effect of warming is to reduce the size of existing areas with sufficient oxygen for a given species. At the same time, populations may move northward along the West Coast to find breathable habitat in colder waters.

While a steady rate of warming can be expected to shrink populations of cold-water fish such as salmon off the West Coast, sudden heat waves — such as "the blob" — could greatly increase the population losses, according to a study led by William Cheung of the University of British Columbia. Climate-change models predict at least four additional "blobs" before the end of the century, he said, although nobody can predict when exactly they will occur.

In the North Pacific, Cheung said pelagic (open water) fish are expected to be most affected by these sudden changes in temperature, with somewhat lesser effects on salmon and bottom fish.

"Our results underscore the need for a reduction of anthropogenic greenhouse gas emissions – the fundamental driver of ocean warming — to limit challenges from marine heat waves on fish stocks and fisheries," Cheung said.

As for what will happen in Puget Sound or any localized area, it would be largely speculation at this point, according to Howard. "One thing we can say," he noted, "is that there will be ecological disruption no matter who wins or loses." ■

This article first appeared in *Salish Sea Currents Magazine.*

A century of warming has reduced dissolved oxygen in Puget Sound

Carr Inlet. Photo: Washington Department of Ecology

A new study outlines the strong link between dissolved oxygen declines and increasing water temperatures, raising questions about the effect of future climate change on Puget Sound.

By Sarah DeWeerdt

WARMING waters likely contribute to decreasing dissolved oxygen levels in Puget Sound, adding another layer of complexity to efforts to understand the health of the estuary and ensure healthy conditions for aquatic life ranging from zooplankton and crabs to salmon and killer whales.

The finding emerges from a preliminary University of Washington analysis of temperature and dissolved oxygen measurements taken at multiple locations in Puget Sound over the past century. The work, which is available on ESS Open Archive but has not yet been peer-reviewed, suggests that increasing temperatures account for roughly half of the dissolved oxygen decline documented in central Puget Sound over the last 100 years.

Puget Sound is “a very complex system that has many other things going on,” says University of Washington doctoral student Dakota Mascarenas, the study’s first author. But, she says, “we've identified a mechanism that, on a century scale, might have about this level of impact.” Mascarenas also presented the unpublished data at an online Science of Puget Sound Water Quality workshop in February.

It’s well known that warmer water holds less dissolved oxygen and other dissolved gases. As water gets warmer, water molecules move faster and jostle against each other more, making it more likely that oxygen molecules will get pushed out of the surface of the water.

Takeaways

- Warming temperatures account for roughly half of the dissolved oxygen decline documented at sites in central Puget Sound over the past century.
- Five Puget Sound monitoring sites have warmed by about 1.4°C over the past 100 years, with oxygen levels declining 0.3-0.9 milligrams per liter per century at three sites.
- The policy implications of these changes are uncertain. Will climate change make Puget Sound more sensitive to nutrient loadings and make action to control human-caused nutrient inputs more urgent? Or will warming simply overwhelm any proposed gains from controlling nutrients?

In fact, scientists have documented temperature-related oxygen decreases at a global scale. There’s widespread concern that climate change and continued increases in temperature could further reduce oxygen levels in marine ecosystems. And so, the look backwards: "The first step in trying to predict the future is to know what happened in the past," says University of Washington oceanographer Parker MacCready, a senior author of the new study.

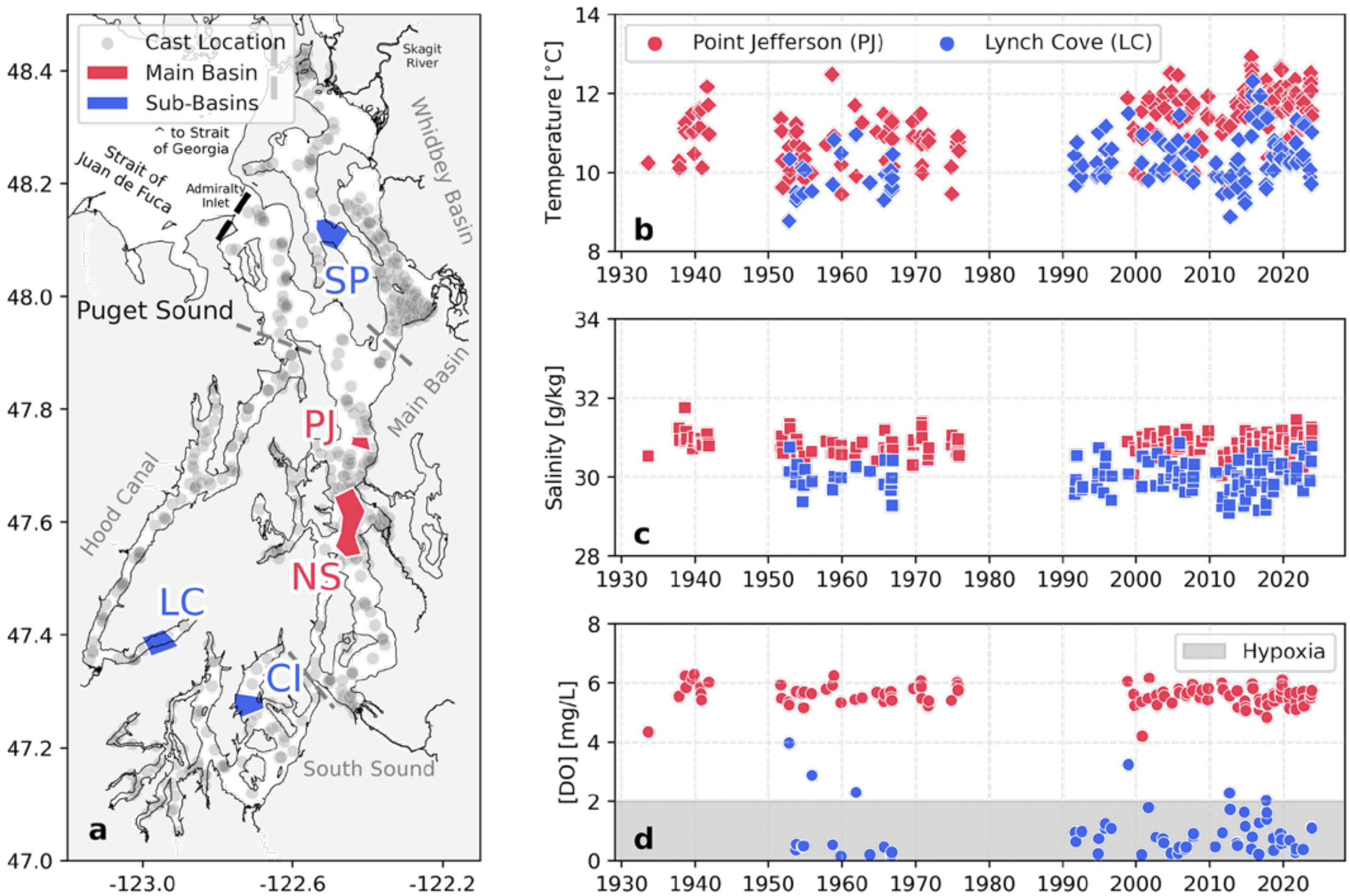
The researchers analyzed more than 12,000 measurements of water quality parameters (temperature, salinity, and dissolved oxygen) dating all the way back to 1932. The measurements were taken near the bottom of the water column in late summer and early fall – where and when low-oxygen conditions are most likely to develop in Puget Sound.

They identified five locations with at least 60 years’ worth of the requisite data: Saratoga Passage in the Whidbey Basin, Lynch Cove in Hood Canal, Carr Inlet in South Sound, and Point Jefferson and a location near Seattle in the Main Basin of Puget Sound.

The long time frame was necessary to discern patterns that transcend the variations in ocean conditions that happen seasonally, from year to year, and on longer cycles (such as the Pacific Decadal Oscillation and El Niño-Southern Oscillation) affecting Puget Sound. “There’s a lot of different timescales of potential variation,” says Mascarenas. “We’ve done our best to look as long as we can.”

The full series of measurements revealed that the five Puget Sound sites have warmed by about 1.4 °C over the past century. This is in line with regional trends in ocean and atmospheric warming.

Meanwhile, dissolved oxygen has decreased at a rate of 0.3-0.9 milligrams per liter per century at the two Main Basin sites. Outside of central Puget Sound, dissolved oxygen trends were more variable: declining at Carr Inlet, stable at Saratoga Passage, and slightly increasing at Lynch Cove.



Map (a) of five Puget Sound data collection locations with sufficient data for century-scale trend analysis (SP= Saratoga Passage, PJ=Point Jefferson, NS=Near Seattle, LC=Lynch Cove. CI=Carr Inlet) and August-November, bottom values at selected sites for (b) temperature, (c) salinity, and (d) DO between 1930 and 2025. Source: Mascareneas et al. 2025 DOI: 10.22541/essoar.174461801.10035683/v1

The researchers then used a well-established equation to calculate the reduction of oxygen in the water, given how much it has warmed. This revealed an expected decrease in dissolved oxygen of 0.31 milligrams per liter per century on average, across all locations.

At Point Jefferson and the near-Seattle location in the Main Basin, this warming-related, expected decline explains 40-100% of the actual decrease in dissolved oxygen observed over the past century. At Carr Inlet, warming accounts for about 50% of the dissolved oxygen loss. Elsewhere, measurements were too variable to draw conclusions.

The marked effect of temperature in explaining oxygen decline was surprising, says MacCready. Although the relationship between temperature and dissolved oxygen is well known, the scientific conversation about dissolved oxygen in Puget Sound has been so focused on nutrient pollution that he hadn't given temperature much thought, he says.

Globally, an estimated 15% of the ocean's oxygen loss between 1960 and 2010 can be attributed to the effects of increasing temperature, according to a report from the International Union for the Conservation of Nature. Warming may explain roughly half of the oxygen loss in the upper 1,000 meters of the ocean, the report says.

Because Puget Sound's Main Basin is deep, contains about 65% of the total volume of Puget Sound, and supplies water to other sub-basins, the Main Basin findings likely reflect changes affecting Puget Sound as a whole, the researchers argue. "That's probably the closest to the background trend that we're going to be able to see," says Mascarenas.

Similar findings have been documented in the Chesapeake Bay – another large estuary adjacent to urban and agricultural development but with a very different structure compared to Puget Sound. This suggests that temperature-related oxygen declines may be a general phenomenon affecting estuaries around the world.

The new study does not make any predictions about how warming may affect dissolved oxygen in Puget Sound in the future, as climate change intensifies. The relationship may not be a linear one and the system could encounter "tipping points" that magnify the effects, Mascarenas says.

The policy implications of these changes are also uncertain. Will climate change make Puget Sound more sensitive to nutrient loadings and make action to control human-caused nutrient inputs more urgent? Or will warming simply overwhelm any proposed gains from controlling nutrients?

What's predictable, for now, is further warming, says MacCready. "There's every reason to think that that trend will continue." ■

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