**Climate-associated change in the abundance of Shrimp in Puget Sound, USA**

Karl Veggerby1, Chelsea L. Wood1, Thomas P. Quinn1, Mark D. Scheuerell1,2

1: School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St, Seattle, WA 98195

2: U.S. Geological Survey Washington Cooperative Fish and Wildlife Research Unit, School of Aquatic and Fishery Sciences, University of Washington, 1122 NE Boat St, Seattle, WA 98195

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**Abstract**

In 2013 through 2016, a severe marine heatwave in the North Pacific, coupled with a strong El Niño event, caused widespread ecological changes along the Pacific coast of North America. Dubbed ‘The Blob’, the marine heatwave has allowed researchers to explore how marine communities change in response to a rapidly warming ocean surface. We used yearly trawl data from 1999–2019 in central Puget Sound to determine whether three species of shrimp, Pink Shrimp (*Pandalus jordani* and *Pandalus eous,* not differentiated here), Spot Shrimp (*Pandalus platyceros*), and Northern Crangon Shrimp (*Crangon alaskensis*) showed an abrupt change in abundance during the 2013–2016 period. In contrast to past El Niño events and warm-phases of the Pacific Decadal Oscillation (PDO) when Pink Shrimp abundance reportedly declined, shrimp abundance increased dramatically in 2013–2015 concurrent with strong El Niño conditions in 2014–2016. Time series analysis demonstrated that annual changes in the catch per unit effort of shrimp were related to a combination of PDO and El Niño signals, but that the relationship was weak, with other environmental factors such as upwelling and predation likely also controlling population dynamics. The cool-phase Pacific Decadal Oscillation immediately prior to the latest El Niño event may have mitigated the expected negative response of several species of shrimp to warmer surface waters in the Puget Sound from the El Niño and the warm Blob.

**Introduction**

In Washington State, shrimp are an important commercial and recreational fishery resource (Smith 1937; Washington Department of Fish and Wildlife 2015; Wargo et al. 2016). Recreational shrimping for several species takes place throughout Puget Sound and along the Washington coast, and a large, stable commercial fishery for Pink Shrimp, *Pandalus jordani*, has operated on the coast since the 1950’s (Wargo et al. 2016; Groth and Hannah 2018). Closely related Northern Pink Shrimp, *Pandalus eous* are caught commercially in smaller numbers in Northern Puget Sound and the Strait of Juan de Fuca (Washington Department of Fish and Wildlife 2022a). The Pink Shrimp fisheries are viewed as extremely productive and sustainable, with abundance driven largely by environmental conditions (Groth and Hannah 2018) such as upwelling intensity (Rothlisberg and Miller 1983), PDO phase (Rothlisberg and Miller 1983; Groth and Hannah 2018), or top-down predation (Hannah 1995). There have been record Pink Shrimp landings in recent years, and the largest landings in the history of the fishery occurred in 2014 and 2015 (Wargo and Ayres 2016).

In 2014 and 2015, a marine heatwave coupled with a strong El Niño increased surface water temperatures of the North Pacific up to 3.9° C above the historical average (National Oceanic and Atmospheric Administration 2019a), causing large-scale shifts in the marine communities (Brodeur et al. 2019). Historically, periods of strong El Niño conditions were followed by large declines in Pink Shrimp abundance, because warm surface water conditions are not favorable for larval shrimp development (Rothlisberg and Miller 1983). The reasons why shrimp appear to have responded differently to the latest strong El Niño are not well understood (Morgan et al. 2019), but are important to identify, so that fisheries managers can anticipate and prepare for rapidly changing ocean conditions.

On the Washington Coast, population trends of Pink Shrimp are well studied (Wargo et al. 2016), but Puget Sound population trends are poorly understood and limited by patchy and incomplete survey data (Don Velasquez WDFW, personal communication). To address this data gap, we present the results of spatially discrete but methodologically consistent sampling over two decades, bracketing the period of intense warming in the coastal ocean. Our specific goal was to determine whether three Puget Sound shrimp species have changed in abundance over time, and if those changes were related to El Niño or PDO cycles (Mantua et al. 1997). We examined data on Spot Shrimp, *Pandalus platyceros* (an exploited fishery in this area), Pink Shrimp, *Pandalus jordani/eous*, (an exploited fishery elsewhere but not in the area where sampling took place), and Northern Crangon Shrimp *Crangon alaskensis* (a species too small to be exploited in fisheries) (Don Velasquez WDFW, personal communication). By reporting data on these three species we intended to consider, though we could not control for, the effects of fisheries on abundance.

**Methods**

Study Area and Sampling Methods

Puget Sound is a complex and highly productive ecosystem in the southern part of the Salish Sea, consisting of several large, environmentally distinct sub-basins (Ruckelshaus and McClure 2007). Puget Sound is heavily influenced by freshwater river discharge, resulting in lower surface salinity and differences in temperature and salinity throughout the year compared with conditions along the Washington Coast (Moore et al. 2008). The surface waters of Puget Sound are generally warmer and have lower salinity than the deeper water flowing into the Puget Sound from the Pacific Ocean (Moore et al. 2008). Our data were collected in Port Madison, a small bay in central Puget Sound, immediately north of Bainbridge Island (Figure 1).

Benthic trawl surveys were conducted in Port Madison between 1999 and 2019 to provide long-term data on the community of nearshore fishes (Essington et al. 2013) and invertebrates (Casendino et al. n.d.), to determine diel changes in distribution (Andrews and Quinn 2012), and to provide training for University of Washington students (Quinn 2015). Surveys were conducted over the course of two days in mid-May of each year, with depths of 10, 25, 50, and 70 m sampled. Over a roughly 24-h period, each of these depths was sampled 5 times, with sequences commencing in the afternoon (14:00), evening (19:00), midnight (0:00), dawn (5:00), and mid-morning (10:00), at the same 4 depth contours.

The trawl survey used a standard Southern California Coastal Water Research Program net, 3.5-m wide, 1-m high, with 35-mm mesh (Essington et al. 2013). For each set, the net was deployed and towed on the seabed for approximately 370 m before being retrieved. All captured fish and invertebrates were placed in live wells, identified to the lowest taxonomic level possible, and released onsite. Metadata (tide, time, depth, and date) were recorded with every tow.

Data Analysis

Of the 25 species of shrimp sampled in Puget Sound, we selected three taxa that were sufficiently abundant (n ≥ 1,500) and for which observations spanned the entire time series. A total of 5,396 Northern Crangon Shrimp (*Crangon alaskensis*), 8,354 Pink Shrimp (*Pandalus eous* and *P. jordani*), and 4,464 Spot Shrimp (*Pandalus platyceros*) were caught in Puget Sound between 1999 and 2019. The species *Pandalus eous* and *Pandalus jordani* were not differentiated in the trawl data, and so were combined as “Pink Shrimp” for the purpose of this study.

Northern Crangon Shrimp (*Crangon alaskensis*) is a small species of shrimp with a maximum size of approximately 50 mm (Wicksten 2012) that occur from the Bering Sea to the Washington Coast (Campos et al. 2012). Species within the *Crangon* genus are widely distributed across littoral and sublittoral zones of the North Pacific and North Atlantic, but generally are not directly targeted by fishers due to their small size. However, their numerical dominance in many areas makes them an ecologically important prey species for many commercially targeted groundfish (Campos et al. 2012).

Ocean Pink Shrimp (*Pandalus jordani*) occur from the Aleutian Islands of Alaska to Southern California (Komai 1999), and are the primary species targeted by the coastal Washington and Oregon Pink Shrimp fishery (Wargo and Ayres 2016). The related species of Northern Pink Shrimp (*Pandalus eous*) is widely distributed across the North Pacific from the Chukchi Sea and the Sea of Japan to the Puget Sound, Washington (Komai 1999) where they are caught commercially around the Strait of Juan de Fuca (Washington Department of Fish and Wildlife 2022a). Spot Shrimp (*Pandalus platyceros*) are large benthic shrimp that grow up to 250 mm in length (Komai 1999) and are distributed from the Aleutian Islands of Alaska to Southern California (Komai 1999). Like Northern Crangon Shrimp, Pink Shrimp and Spot Shrimp are important prey species for many commercially targeted flatfish such as Pacific Hake, *Merluccius productus* (Hannah 1995).

Northern Crangon Shrimp are too small to be of recreational or commercial interest. Both Spot and Pink Shrimp are highly valued commercial and recreational targets. The marine management unit where our trawls were conducted has a limited recreational fishery for Spot Shrimp (Washington Department of Fish and Wildlife 2022b), and a First Nation treaty fishery for Spot Shrimp (Washington Department of Fish and Wildlife 2022a, Daniel Sund WDFW, personal communication). Most commercial Pink and Spot Shrimp efforts within Puget Sound are concentrated farther North of the study area near the San Juan Islands (Washington Department of Fish and Wildlife 2022a), so we expect that the effect of exploitation on our study species to be minimal (Don Velasquez WDFW, personal communication).

We extracted the Oceanic Niño Index and Pacific Decadal Oscillation values from NOAA’s Climate Prediction Center (National Oceanic and Atmospheric Administration 2019a) and NOAA’s National Centers for Environmental Information (National Oceanic and Atmospheric Administration 2019b), respectively. Monthly Oceanic Niño Index and Pacific Decadal Oscillation values were averaged over the previous 12 months from each year’s sampling effort (i.e., May of year *t-1* through April of year *t*).

Shrimp catch numbers were aggregated by year across both sampling time and sampling depth for each species. We fit different forms of a random walk model to the time series of shrimp catches to examine 1) whether annual catch per unit of effort (CPUE) values had any systematic trends; 2) whether any CPUE trends were common among all species or separate; and 3) whether any trends over time were related to the ONI and PDO. We then evaluated the data support for each form of model using Akaike’s Information Criterion corrected for small sample size (AICc). All CPUE data were log-transformed prior to analysis to meet assumptions of normally distributed errors.

For a single time series *i*, we modeled the log-CPUE at time *t* (*xi*,*t*) as a biased random walk, whereby

*xi*,*t* = *xi*,*t*-1 + *ui* + *wi*,*t* (1)

and *ui* is the upward or downward bias (trend). We assumed that the errors were normally distributed, such that *wi*,*t* ~ N(0, *qi*), and residuals were examined with a Q-Q plot to verify that this assumption held. For models that included the ONI or PDO as drivers of abundance, the single bias term in equation (1) was replaced by the estimated effect (*bk*) of the specific covariate *k* at time *t* (*ck*,*t*), such that

*xi*,*t* = *xi*,*t*-1 + *bk* *ck*,*t* + *wi*,*t* (2)

The biased random walks given by (1) and (2) were then compared to a simple random walk where either *ui* = 0 or *bk* = 0.

Because our trawl data were an incomplete census of the true population size, we included an additional data model within a state-space framework to account for sampling (observation) errors. Specifically, we assumed that the estimated log-CPUE for genus *i* at time *t* (*yi*,*t*) was equal to the true log-CPUE plus an offset (*ai*) and some sampling error (*vi*,*t*), such that

*yi*,*t* = *xi*,*t* + *ai* + *vi*,*t* (3)

and the observation errors were independent and identically distributed with *vi*,*t* ~ N(0, *r*).

To evaluate whether any of the genera shared common trends in catches over time, or whether any bias in the trends was common to all genera, we fit multivariate forms of the models specified in equations 1-3. When all three taxa have unique bias terms, the random walk model is given by

(4)

where *C* denotes *Crangon*, *Pej* is for *Pandalus eous* plus *Pandalus jordani*, and *Pp* is for *Pandalus platyceros*. The model changes slightly when all three taxa are assumed to have the same bias, such that

(5)

The multivariate model with unique effects of a single covariate (*ck*) on each taxa is then

(6)

When the effects of the single covariate are the same for all taxa, the model simplifies to

(7)

Similarly, the model with unique effects of two covariates is given by

(8)

When the effects of the two covariates are shared among taxa, the model simplifies to

(9)

For models where we assume two states represented by the two genera, the biased random walk is given by

(10)

where *C* denotes *Crangon* and *P* is for *Pandalus*. The model changes slightly when both genera are assumed to have the same bias, such that

(11)

The multivariate model with covariates is then

(12)

when the effects of the covariate are different for the two genera, or

(13)

when the effects of the covariate are the same for the two genera.

The observation model for the case where all three taxa are assumed to have their own unique state is given by

(14)

For the cases where the states are grouped by the two genera, the observation model is

(15)

When all three taxa are assumed to be observations of a single state, the model becomes

(16)

We fit all models with version 3.11.3 of the MARSS package (Holmes et al. 2020) for the R software (R Core Team 2022). All data and code necessary to reproduce our analyses and results are available on GitHub at https://github.com/veggerk/Puget-Sound-shrimp-paper.

**Results**

*Crangon* Shrimp abundance began to increase around 2010 and remained high through the end of the dataset in 2019 (Figure 2). Both Pink Shrimp and Spot Shrimp abundances increased dramatically in 2013 and remained high through the end of the dataset in 2019 (Figure 2). CPUE of Spot Shrimp varied more since 2013, and 2015 was similar to pre-2013 levels. Abundance subsequently increased again, and 2019 Spot Shrimp CPUE from our Port Madison trawl was the highest on record.

Model selection results showed a negligible difference in data support for two models that were within delta AICc of 2.0 of each other (Table 1). The first model (delta AICc 1.1) contained a single common state shared by all genera, a downward bias of -0.207 (SE: 0.038) driven by the Pacific Decadal Oscillation, and an upward bias of 0.201 (SE: 0.127) driven by the El Niño cycle (Figure 3). When Pacific Decadal Oscillation values were negative (cool phase) shrimp abundance increased. Positive ONI values were associated with increasing shrimp abundance, with the trend largely being driven by the strong El Niño in 2014–2016 concurrent with a large increase in shrimp abundance that began in 2013 (Figure 2). The second model (delta AICc 0.0) contained a common state shared by all genera, and an upward bias term of 0.122 (SE: 0.015) with no added covariates (Figure 3).

**Discussion**

The positive association of CPUE for all three of the focal shrimp species sampled in Port Madison to warmer-than-average temperatures during 2014–2015 agree with the observations of Groth and Hannah (2018), who noted that Washington coast Pink Shrimp responded differently to this latest phase of warmer water compared to prior events where growth and abundance were depressed during warm periods (Rothlisberg and Miller 1983). Previous analysis has indicated that warmer water from El Niño and/or warm phase PDO events can depress Pink Shrimp growth and abundance (Rothlisberg and Miller 1983). The specific mechanisms that caused shrimp to respond differently in 2014–2016 were previously unknown, but our data suggest that it may be related to different climate dynamics during the 2014–2016 El Niño compared to the previous significant El Niño events in 1982–1983 and 1997–1998 (Jacox et al. 2016; Groth and Hannah 2018), which occurred concurrently with a long-term warm phase of the Pacific Decadal Oscillation. The abundances of shrimp observed in Puget Sound have not returned to their pre-2013 levels as of 2019, even though the El Niño phase and The Blob ended in 2016, indicating that this may be an example of a long-term community shift. In fact, Spot Shrimp CPUE from 2019 was higher than the initial 2013 increase. However, our sampling did not cover Puget Sound, in terms of its horizontal or vertical extent. Shrimp abundance in areas deeper than 70m were not sampled as part of this study.

In contrast to the increases in abundance seen in this study, Brodeur et al. (2019) observed a decrease in the abundance of krill and shrimp in the unusually warm surface and mid-waters in the California Current during The Blob event. However, Brodeur et al. (2019) noted that their trawl surveys were conducted in the warmer upper layers of water above the thermocline, and thus could not ascertain the community composition in deeper layers, which may have not been as affected by The Blob since the largest temperature differences as a result of The Blob occurred in the top 50–80 m of water, with deeper temperatures remaining close to their long-term mean along the Washington Coast (Peterson et al. 2017; Auth et al. 2018). Paired acoustic data from the same study showed anecdotal evidence of possible aggregations of euphausiids and other micronekton below the warmer surface layer of water (Brodeur et al. 2019), indicating possible changes in shrimp and krill diel vertical behavior in response to unfavorable temperatures near the surface.

Changing environmental conditions have shifted spatial distribution and abundance of shrimp and other marine invertebrate populations elsewhere (Sakuma et al. 2016; Peterson et al. 2017; Brodeur et al. 2019). For example, the abundance of shrimp, krill, and other crustaceans declined in the surface and midwaters off the Washington coast during the 2014–2015 Blob event, in conjunction with a dramatic increase in the abundance of warm-water gelatinous organisms (Sakuma et al. 2016; Brodeur et al. 2019), and a decline in marine biomass of salmon (Cheung and Frolicher 2020) associated with a lack of high-quality marine prey (Daly et al. 2017). The invertebrate community still has not returned to historical levels of abundance and composition, and the shift may be permanent (Brodeur et al. 2019). These changes may be due to a decline in absolute abundance, or a shift in habitat usage (Brodeur et al. 2019). For example, Pink Shrimp move up in the water column at night to feed but may have begun to avoid surface waters that were unfavorably warm (Brodeur et al. 2019).

In our models for the temporal dynamics of shrimp CPUE, the Pacific Decadal Oscillation and El Niño signals were associated with increases in shrimp abundance. The Pacific Decadal Oscillation was generally in a cool phase from 1998 to 2014 and reached its lowest coolest phase value since the 1950’s in 2012 (National Oceanic and Atmospheric Administration 2019b). This cool phase Pacific Decadal Oscillation also roughly coincided with a strong La Niña in 2010 to 2011 (National Oceanic and Atmospheric Administration 2019a). Given that Pink Shrimp mature in 1–2 years, the overlapping strong La Niña and strong cool phase Pacific Decadal Oscillation in 2010 and 2011 likely created ideal conditions which led to the increase in adult shrimp observed 2 years later in 2013. Shrimp abundance remained elevated through the following El Niño in 2014–2016, with the random walk model predicting a positive relationship between shrimp abundance and El Niño conditions. This surprising result was mainly driven by this 2014–2016 El Niño concurrent with high shrimp abundance. However, the effects of PDO and ENSO were somewhat weak, suggesting there are other, unmeasured environmental factors such as upwelling intensity (Rothlisberg and Miller 1983) or top-down predation by groundfish (Hannah 1995) that also significantly mediate shrimp abundance.

As environmental conditions shift over the coming decades, there will be winners and losers among species (Fabricius et al. 2011). Those that can tolerate or even thrive in warmer, more acidic waters may expand their ranges and increase in abundance (Hendriks et al. 2010). Although the species studied here showed a positive response in abundance during periods with warmer than average temperature, previous responses of Pink Shrimp to El Niño and Pacific Decadal Oscillation have been negative, possibly due to longer warm phases of the Pacific Decadal Oscillation concurrent with El Niño. It is also important to note that temperature is not the only aspect of the marine environment predicted to change in the coming decades. Predicted changes in ocean acidity under future climate change scenarios (Caldeira and Wickett 2005; Orr et al. 2005; Cao and Caldeira 2008; Steinacher et al. 2009) could offset or reverse the trends seen in this study, as acidic water hampers shell formation of calcifying organisms (Orr et al. 2005). In addition to temperature and pH changes, natural and anthropogenically mediated hypoxia is also projected to increase (Rabalais et al. 2010; Doney et al. 2012). Ocean acidification and hypoxia are known to be coupled and the negative impacts on marine organisms are synergistic (Rabalais et al. 2010).

Pink and Spot Shrimp are important components for the Washington State recreational and commercial shrimp fisheries. Interest in both the commercial and the recreational fisheries is increasing as the value of shrimp has gone up, with catch quotas for Spot Shrimp usually reached in recent years (Don Velasquez WDFW, personal communication). Although, all commercial shrimp fisheries in Washington State are limited entry, with resource utilization from the commercial sector roughly capped in Puget Sound (Daniel Sund WDFW, personal communication). Pink Shrimp in Puget Sound are understudied compared to coastal stocks in Washington and Oregon which have been the focus of extensive research and monitoring (Wargo et al. 2016). Given the increasing interest in Puget Sound shrimp stocks, these species are good candidates for future research efforts.

Although the ultimate effect of climate change on these species is unclear, judging by the negative responses to increased average water temperatures during concurrent warm phase Pacific Decadal Oscillation periods and El Niño, a shift in abundance will likely occur in the coming decades as average sea surface temperatures begin to mirror what currently would be considered above average or extreme. In particular, periods of warm phase Pacific Decadal Oscillation patterns will likely be correlated with a reduction in shrimp abundance. This study provides a brief analysis of possible environmental drivers of shrimp abundance, as well as 21 years of time series data on abundance of several common shrimp species in Puget Sound in an area where previous survey data are limited or non-existent.

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**Data availability**

All data used in this study is available online at zenodo.org, DOI: insert DOI here when paper is submitted.

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Table 1.

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| Delta AICc | covariates | Form of bias | # states | covariate effect |
| 0 | none | Simple | 1 | N/A |
| 1.1 | PDO + ENSO | *f*(covariates) | 1 | shared |
| 2.1 | PDO | *f*(covariates) | 1 | shared |
| 2.3 | none | Simple | 2 | N/A |
| 3.5 | PDO | *f*(covariates) | 2 | shared |
| 3.5 | PDO + ENSO | *f*(covariates) | 2 | shared |
| 4.6 | none | Simple | 2 | N/A |
| 4.7 | none | Simple | 3 | N/A |
| 5.0 | none | none | 1 | N/A |
| 5.9 | PDO | *f*(covariates) | 2 | unique |
| 5.9 | PDO | *f*(covariates) | 3 | shared |
| 6.0 | PDO + ENSO | *f*(covariates) | 3 | unique |
| 6.8 | ONI | *f*(covariates) | 1 | shared |
| 7.9 | PDO + ENSO | *f*(covariates) | 2 | unique |
| 9.8 | none | Simple | 3 | N/A |
| 11.1 | PDO | *f*(covariates) | 3 | unique |
| 13.0 | none | none | 2 | N/A |
| 14.6 | ONI | *f*(covariates) | 2 | shared |
| 16.4 | PDO + ENSO | *f*(covariates) | 3 | unique |
| 16.7 | ONI | *f*(covariates) | 2 | unique |
| 22.8 | none | none | 3 | N/A |
| 24.2 | ONI | *f*(covariates) | 3 | shared |
| 29.1 | ONI | *f*(covariates) | 3 | unique |

Map

Description automatically generated

Figure 1. Map of Puget Sound, Washington, USA, with study area highlighted.



Figure 2. Catch per unit effort (CPUE) in May each year of the primary three species of shrimp caught in Port Madison, Puget Sound bottom trawls from 1999 to 2019.



Figure 3. (A) Time series of standardized shrimp log-CPUE (colored points) and the best fit model that included the Pacific Decadal Oscillation and ONI as drivers of change over time (black line). (B) Time series of standardized shrimp log-CPUE (colored points) and the most parsimonious best fit model that contained only a bias term to explain drivers of change over time (black line).