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

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**Abstract**

In 2013 through 2016, a severe marine heatwave in the North Pacific coupled with a strong El Niño event to cause 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 study long-term trends in the abundance of three species of shrimp, Pink Shrimp (*Pandalus jordani*), Spot Shrimp (*Pandalus platyceros*), and Northern Crangon Shrimp (*Crangon alaskensis*) to determine whether they 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 [yes? Not our data, right?] 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 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 from the El Niño and the warm blob. [probably should indicate whether Puget Sound was warm in these years or not]

**Introduction**

In Washington State, shrimp are an important commercial and recreational fishery (Wargo et al. 2016). Recreational shrimping for several species takes place throughout Puget Sound and across the outer coast of Washington, while a large, stable commercial fishery for Pink Shrimp, *Pandalus jordani*, has existed on the coast of Washington since the 1950’s (Wargo et al. 2016; Groth and Hannah 2018). The Pink Shrimp fishery is viewed as extremely productive and sustainable, with abundance driven largely by environmental conditions (Groth and Hannah 2018). 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 to increase 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. [No mention is made of diel vertical migration, yet this is listed among the keywords so we either need a hypothesis or it should be deleted. Otherwise, the readers are misled.]

**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 et al. 2007). 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 (e.g., Essington et al. 2013) and invertebrates (e.g., Casendino et al. in review), to determine diel changes in distribution (e.g., 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, in the afternoon, evening, middle of the night, dawn, and mid-morning, 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. [I think it is important to note that Crangon are too small to be taken in sport or commercial fisheries whereas spot prawns definitely are a prime target. I am not sure about pinks. Thus some mention should be made here or in the Introduction to this effect, and any interpretation should also consider exploitation. WDFW must have information on the extent of that, in Area 10 and Puget Sound as a whole. We will need to link that to recruitment, etc. The finfish are virtually closed to fishing but I know there are tribal crab fisheries in Port Madison. I do not know about prawns.]

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*). [OK but what about Puget Sound conditions? Surely there are data from most of the years on temperature? See Smith et al. (2015) for links to Puget Sound data.

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) [Were catches pooled so the annual total was the unit or replication? I think this needs to be clear. If so, then there is no information on vertical distribution or diel changes. That is your choice but it needs to be clear.]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*). 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 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).

So, no mention of depth distribution or diel changes? That is fine, but it leaves a lot of data unreported. Given that there are depths in Puget Sound greater than we trawled, and given the ease of producing such a table, perhaps you can produce a normalized table of catch per trawl by depth and time of day. That is, a 4 x 5 table with the average percent of all shrimp taken in each depth x time combination, so the total is 100% for each year, averaged over the years (unless you want to ask whether this too has changed). For example, if the highest catches are at the greatest depth, then one might wonder whether the shrimp are just a bit deeper or shallower in some years, not more or less abundant. I know if I were a reviewer, I would ask about this. There could be, for example, 3 supplemental tables, one for each species, or one larger one. More analysis of changes in depth distribution by year would also be possible, and would be revealed quickly from the assembly of the data into such a table. If there is no change then that is that, but if there is a change (i.e., mode at 50 m in some years vs. 70 m in others, etc.), that might be worth mentioning. Shrimp go pretty deep; along the coast they are well beyond our depths.

**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 [this reference is incomplete]. 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. [Be careful – our sampling did not cover Puget Sound, in terms of horizontal or vertical extent.]

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.[This text will cause the reader to wonder about physical conditions at our site. Perhaps you do not wish to use the annual surface temps or depth profile data, but at least some mention of general physical conditions such as temperature and salinity seems called for. I think that belongs in the Methods section under site description, or the Results, depending on how the paper is cast and if/how such physical data are used. Puget Sound is quite different from the coastal ocean, and readers will need to know this.

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 [should this be “Blob” here or elsewhere?] 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). OK but that is the Pacific Ocean, and we are a long way from there. Maybe emphasize the need for comparative work in the Salish Sea. Speaking of which, have the Canadian (DFO, etc.) done similar shrimp work? It would not surprise me.]

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 and was partly responsible for 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 that also 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).

Pink and Spot Shrimp are an important resource for recreational and commercial fisheries. Interest in both the commercial and the recreational fishery is increasing as the value of shrimp has gone up, with catch quotas usually reached in recent years (Don Velasquez WDFW, personal communication). 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 driver of shrimp abundance, as well as 21 years of time series data on abundance of three common shrimp species in Puget Sound in an area where previous survey data are limited or non-existent.

**Acknowledgements**

The sampling described herein was supported as part of the teaching program at the University of Washington’s School of Aquatic and Fishery Sciences (SAFS), and we are grateful for SAFS’ commitment to experiential learning. The vessel from which almost all sampling took place was owned and operated by Charles Eaton, and we appreciate his skillful operation and assistance with species identification, as well as the help from the dozens of teaching assistants and hundreds of students over the years. We also thank the crew of the R/V Rachel Carson, which is the current platform for sampling and which contributed data in 2019. Additionally, we thank Don Velasquez and Daniel Sund for their advice and expertise. This research was funded by the School of Aquatic Fisheries Sciences, University of Washington. CLW was supported by a CAREER Award from the US National Science Foundation Division of Environmental Biology (NSF Grant Number 2141898), a Research Grant from the Cooperative Institute for Climate, Ocean, and Ecosystem Studies (CICOES), a University of Washington (UW) Innovation Award, and the UW Royalty Research Fund. None of the authors has a conflict of interest associated with this study.

**Data availability**

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

**References**

There are quite a few typos and mistaked in the citations and you might want to fix them in your database, but might also break the link so you can fine-tune it for the journal’s format. E.g.,

All scientific names in italics (e.g., Groth and Hannah, journal titles not in all caps (e.g., Rothlisberg), “Atmospheric” in Ruckleshaus. Groth and Hannah is incomplete too.

Also, perhaps cite these for the basic methods, goals, etc. of the sampling:

Andrews, K. S., and T. P. Quinn. 2012. Combining fishing and acoustic monitoring data to evaluate the distribution and movements of spotted ratfish *Hydrolagus colliei*. Marine Biology 159:769-782.

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And look at this for a link to data on Puget Sound temperatures

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Also, and importantly, I think the readers need to know more about these animals in terms of depth distribution, population regulation, links to climate, and fisheries. I am sending a few papers I came across in a quick Google Scholar search but this is not my field, by a long shot.

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Table 1.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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).