Fall 2022

Avian and Shallow Water Community Response to Pacific Herring (Clupea pallasii) Spawn Events

Heidi Stewart
Western Washington University, elaine.heidi@gmail.com

Recommended Citation

Stewart, Heidi, "Avian and Shallow Water Community Response to Pacific Herring (Clupea pallasii) Spawn Events" (2022). *WWU Graduate School Collection*. 1146.
https://cedar.wwu.edu/wwuet/1146

Avian and Shallow Water Community Response to Pacific Herring (*Clupea pallasii*) Spawn Events

By

Heidi Stewart

Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

ADVISORY COMMITTEE

Dr. Kathryn L. Sobocinski, Chair

Dr. Todd Sandell

Dr. M. Brady Olson

GRADUATE SCHOOL

David L. Patrick, Dean

Master's Thesis

Heidi Stewart

November 28, 2022

Avian and Shallow Water Community Response to Pacific Herring (*Clupea pallasii*) Spawn Events

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Heidi Stewart
November 2022

Abstract

Pacific Herring play a critical role in the food web of the Salish Sea. The Cherry Point stock, centered 30 miles north of Bellingham Bay, has declined roughly 97% since the 1970s. This massive decline is a point of concern for environmental and fishery managers and has led to research into both the initial decline and the stock's inability to recover. One key data gap in need of research is whether the Cherry Point herring stock is experiencing increased predation from the nearshore fish, bird, and invertebrate community due to its unique late spawn timing and spawning behavior. To that end, I investigated predation on herring spawn by deploying predator exclusion enclosures and remote underwater time lapse cameras at spawning locations of both the declining Cherry Point stock and Semiahmoo Bay, a nearby stock with stable population trends. Bird surveys in 2021 indicate that avian abundance was highest before spawning occurred and that most birds had left the spawning area before eggs were deposited. The exclusion of avian, large fish, and invertebrate predators from accessing the eggs did not significantly affect the survival of eggs when compared to areas exposed to predation from these groups. There was significant egg mortality in both the control and excluded plots over the spawning period. Remote underwater time-lapse cameras showed higher abundances of fish predators and greater predator diversity at the Cherry Point spawning site compared to Semiahmoo Bay, but this could be driven by seasonal differences. A non-metric multidimensional scaling analysis of the time-lapse data showed slight differences between pre-spawn predator assemblages and predator assemblages during and after the incubation period. This study shows that while predation from larger fauna did not have a significant impact on Pacific Herring egg survival for the years of 2021 and 2022, egg mortality was high and is likely influenced by a multitude of factors including spawning time and habitat, water temperature, and numerous smaller fish and invertebrate species that take advantage of the lipid-rich food source.

Acknowledgements

Many thanks to Dr. Kathryn Sobocinski for her mentorship and support throughout this process as well as my committee members for their time and effort in reviewing this manuscript. Additionally, thanks to Dr. Todd Sandell for his guidance and mentorship in the field; Meghan Bugaj, Garrett Klee, Anthony Tulloch, Emma Owens, Mae Brenneman, and Megan O’Hara for their field support; and Lucy Greeley and Alex Haase for their assistance in data processing. This study was funded by Puget Sound Partnership, WWU Huxley Small Grant, and WWU Research and Sponsored Programs.

Table of Contents

Abstract ---------- **iv**

Acknowledgements ---------- **v**

List of Tables and Figures ---------- **vii**

Introduction ---------- **1**

Methods ---------- **7**

- Study Site ---------- 7
- Exclusion Experiment ---------- 9
  - Field ---------- 9
  - Laboratory ---------- 10
- Remote Underwater Time-lapse Cameras ---------- 11
- Analysis ---------- 12

Results ---------- **15**

- Exclusion Experiment ---------- 17
- Remote Underwater Timelapse Cameras ---------- 21
- Environmental Variables ---------- 27

Discussion ---------- **31**

- Mortality and Predation ---------- 31
- Shallow-water Assemblage and Habitat Use ---------- 33
- Other Sources of Mortality ---------- 34

Conclusions ---------- **37**

References ---------- **38**

List of Tables and Figures

Figure 1: Pacific Herring spawning biomass in the Southern Salish Sea -- 2
Figure 2: Historical spawning locations in 1974, 1994 and 2014 -- 3
Figure 3: Site map of experiment and camera deployment locations --- 8
Figure 4: Retrofitted sablefish pot -- 10
Figure 5: Pacific Herring eggs collected in spring 2022 -- 11
Figure 6: Remote underwater timelapse camera --- 12
Figure 7: GLM of egg density by experiment --- 16
Figure 8: LM of percent cover by experiment --- 17
Figure 9: LM of percent cover by experiment and treatment --- 18
Figure 10: GLM of egg density by treatment --- 19
Figure 11: Boxplots depicting egg densities -- 19
Figure 12: GLM of egg density by experiment and treatment -- 20
Figure 13: Frequency of occurrence of predators by stock --- 23
Figure 14: Scatter plot of predator abundance -- 23
Figure 15: Frequency of occurrence of predators -- 25
Figure 16: Frequency of occurrence of predators by year -- 25
Figure 17: Scatter plot of a nMDS analysis of spawn period --- 26
Figure 18: Scatter plot of a nMDS analysis of year --- 27
Figure 19: Tidal height by predator abundance --- 28
Figure 20: Tidal height by time of day and abundance --- 28
Figure 21: Scatter plot of temperature by Julian day --- 29
Figure 22: Scatter plot of predator abundance and temperature --- 30
Figure 23: Scatter plots of temperature, day, and predator abundance ------------------------------------ 30

Table 1: Average percent of unviable Pacific Herring eggs -- 21
Table 2: All species observed with the time-lapse camera --- 21

Equation 1: Suface Area --- 10
Equation 2: GLM --- 13
Equation 3: nMDS Stress -- 14

Introduction

Small but significant, forage fishes occupy a crucial position in marine food webs that link energy from plankton to fish, birds, and mammals (Pikitch et al. 2012, 2014). In many cases, forage fishes are the majority of prey for iconic, ecologically important, and commercially valuable upper trophic level species (Pikitch et al. 2012). Forage fishes are characterized by small body size, rapid growth, and strong responses to environmental variability (Pikitch et al. 2012). In the Salish Sea, Pacific Herring (*Clupea pallasii*) provide an essential function by transferring large amounts of energy from primary producers and zooplankton to upper trophic levels as prey, and as a migratory fish, by transferring energy and biomass from the coastal zone to offshore and inland waters (Pikitch et al. 2014, Surma et al. 2018a, 2018b, Fox et al. 2018). As prey for many pelagic, nearshore, and terrestrial species, they play a pivotal role in food web ecology and are important indicators of the health and productivity of the Salish Sea (Willson et al. 1998, Willson and Womble 2006, Lok et al. 2008, Schweigert et al. 2010, Fox et al. 2018, Puget Sound Partnership 2022). Sea birds rely on herring eggs for overwintering, recently hatched larvae and juveniles are important prey for emigrating salmon, and adult herring provide important prey resources for cetaceans, pinnipeds, and predatory fish (The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018). As a foundational species in the Salish Sea and beyond, it is critical that Pacific Herring populations are managed in a sustainable way.

Not only do forage fishes play a direct role in ecosystem trophic dynamics, they also play an indirect role in tribal, commercial, and recreational fisheries as important prey for desirable piscivorous fish (Surma et al. 2021). It’s been estimated that forage fishes provide about $16.9 billion USD to global fisheries annually (Pikitch et al. 2014). The combination of natural mortality from predation and exploitation from fishing has been hypothesized to amplify population fluctuations (Shelton and Mangel 2011, Siple et al. 2018). In Washington State, Pacific Herring have highly variable population abundances that can fluctuate significantly over short (interannual) and long (decadal) time scales (Siple et al. 2018).

It’s important to note that, even when isolated from fishing mortality, these fluctuations in population size are common in marine fishes and are induced by changes in the rates of their growth, reproduction, age structure, and survival (Landis and Bryant 2010, Siple et al. 2018). When looking across longer time scales, most stocks of Pacific Herring in the Southern Salish Sea are on a downward trend (Figure 1; Siple et al. 2018, The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018, Sandell et al. 2019)

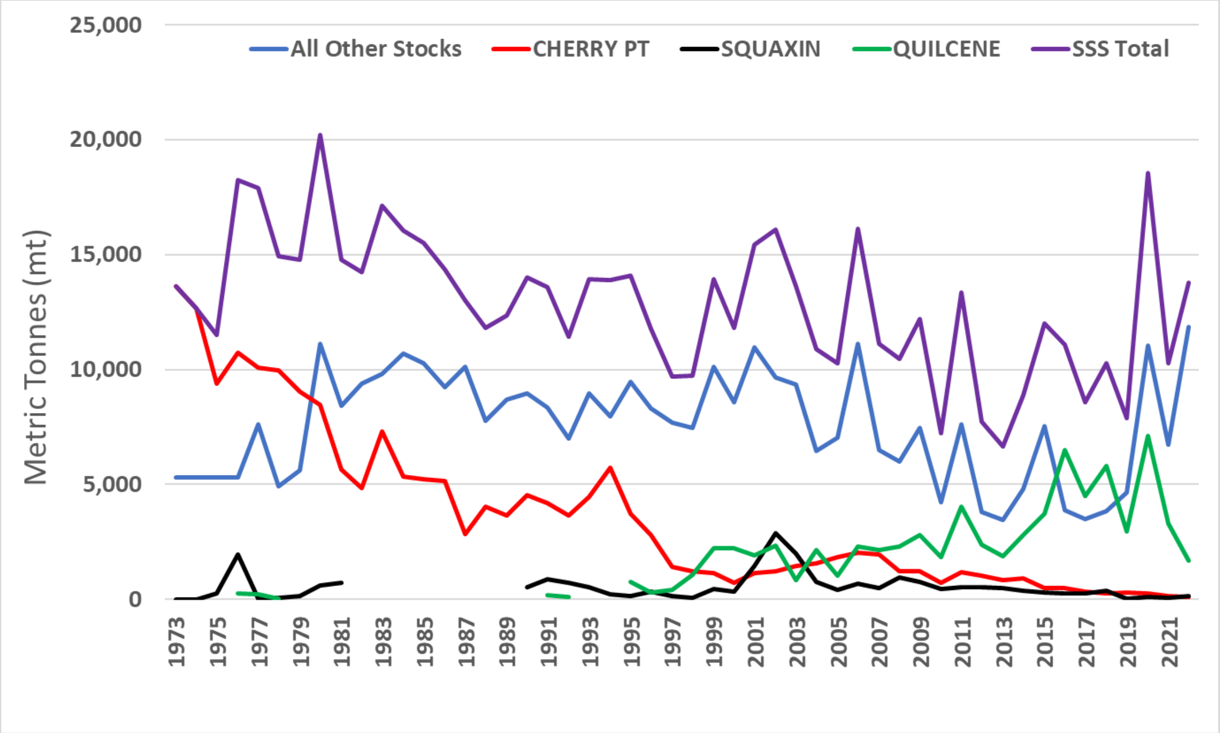

Figure 1: Pacific Herring spawning biomass in the Southern Salish Sea. Stocks traditionally considered genetically unique (Cherry Point and Squaxin Pass) and increasing stocks (Hood Canal) have been separated to show biomass differences (Sandell et al. 2019).

This downward trend is driven by the massive decline of the Cherry Point stock, which was once the most abundant in U.S. waters but has declined by over 97% since 1973 (Sandell et al. 2019). The spawning location for the Cherry Point stock historically spanned from Point Roberts, WA to northern Bellingham Bay and Lummi Island, WA. Since the 1970s, the spawning area has significantly contracted and, in recent years, spawn has been mostly observed at Birch Head, WA (Figure 2; Sandell et al. 2019). In 2016, the Cherry Point stock was categorized as depressed with no signs of recovery (Sandell et al.

2019). This stock is temporally isolated and genetically distinct from the other stocks in the southern Salish Sea, with a significantly later spawning period in mid-April through May, instead of the typical January through early April spawning period seen in other regional stocks. This late spawning time provides an important prey resource for emigrating salmon and migrating Surf Scoters (*Melanitta perspicillata)* not offered by the earlier spawning events. This unique life-history coupled with its continued decline has made the Cherry Point stock an area of significant concern for the research community.

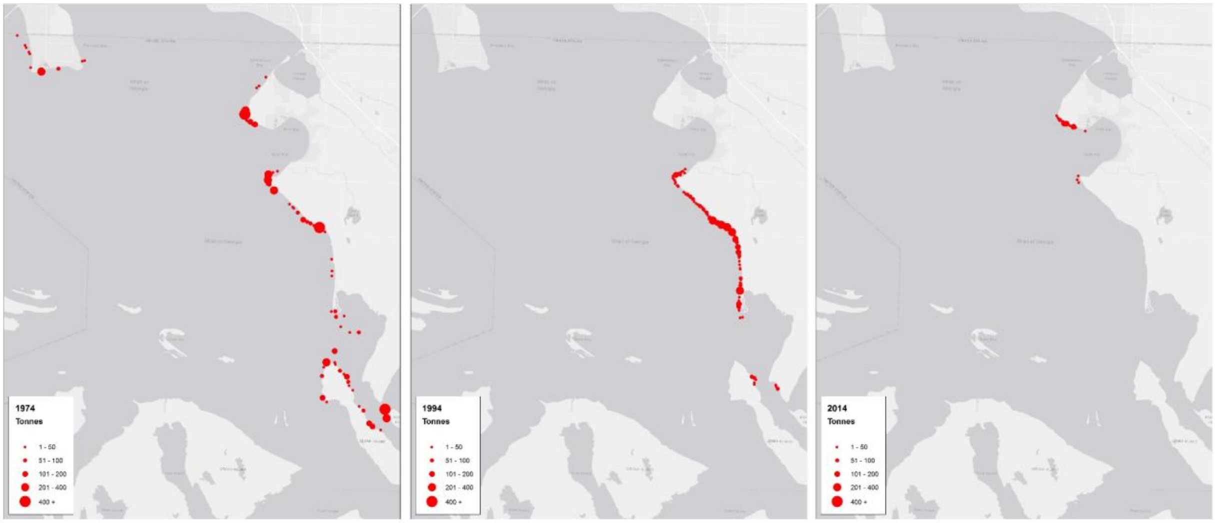

Figure 2: Historical spawning locations in 1974, 1994 and 2014 showing the contraction of spawning area through time (Sandell et al. 2019).

Investigation into the cause of the decline and the lack of recovery in the Cherry Point stock has been the focus of much research in recent years. In the early to mid-1970s many of the stocks in Puget Sound, including Cherry Point, demonstrated an age structure collapse (Landis and Bryant 2010) but it is thought that the causative agent must have effected these stocks on the scale of the Puget Sound, since the collapse in age structure was widespread (Landis and Bryant 2010). While the cause of the initial decline has been well studied, less research has focused on the Cherry Point stock’s lack of recovery, but the stock’s unique spawning time has raised concerns regarding impacts on its early life history, particularly the recruitment from eggs to larval fish.

Adult herring typically congregate near their spawning grounds several weeks prior to spawning and although we do not have a firm understanding on how they determine when to spawn, temperature is likely a factor (Haegele and Schweigert 1985). Spawning grounds are typically found in high energy environments in nearshore, tidally-active areas, with macrophytes used as spawning substrate (Haegele and Schweigert 1985, Fox et al. 2018). In the Salish Sea, female herring often deposit their eggs on seagrass (*Zostera marina*), brown algae (*Sargassum muticum*), and red algae (*Mazzaella splendens*) while male herring broadcast milt alongside (Haegele et al. 1981, Haegele and Schweigert 1985, Shelton et al. 2014). The distribution of eggs is usually dependent on the substrate type and the slope of the beach (Haegele and Schweigert 1985). Within the Cherry Point stock, spawning typically occurs in two separate events ("waves") and eggs from each wave take approximately 2 weeks to hatch, which is generally dependent on water temperature (Kawakami et al. 2011). This stock also tends to spawn in very shallow depths that are often exposed at low tides and are susceptible to high wave energy due to its location in a high energy zone. Egg mortality varies considerably across subpopulations in the Salish Sea but generally occurs due to silting, wave action, desiccation from air exposure, and predation (Haegele and Schweigert 1985, Shelton et al. 2014). Few studies have been done in the Salish Sea to quantify egg predation but there is evidence that predation could be a source of significant egg loss for some populations (Haegele and Schweigert 1990, Haegele 1993, Rooper and Haldorson 1999, Bishop and Green 2001, Willson and Womble 2006, Kotterba et al. 2017).

Over 25 species of birds have been documented in large numbers at Pacific Herring spawning sites feeding on the herring themselves and/or their eggs (Rooper and Haldorson 1999). Both resident and migratory seabirds are highly dependent on Pacific Herring spawn and have been found to alter their movements and habitat use to take advantage of these events (Lok et al. 2008, 2012, Anderson et al. 2009). Scoters (*Melanitta* spp.), a type of sea duck, have been found to alter their diet from bivalves (their typical winter diet) to herring eggs in the spring (Lewis et al. 2007). Herring eggs are rich in lipids and because of high spawn densities are often much easier to forage for than bivalves, allowing scoters to meet energetic demands with reduced effort (Lewis et al. 2007). This is especially important in the spring as migration starts. The phenomenon of scoters “riding the silver wave” of herring spawn to their breeding grounds is well documented (Lok et al. 2008, Anderson et al. 2009). Prolonged declines in forage fishes have been shown to compromise the long-term breeding success of seabirds (Cury et al. 2011). This huge demand for herring eggs has been found to have a significant effect on the recruitment of eggs into larval fish for years with low herring spawn densities (Bishop and Green 2001, The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018).

Migrating Surf (*Melanitta perspicillata*), White Wing (*Melanitta deglandi*), and Black (*Melanitta americana*) Scoters enter the Salish Sea from mid-April to mid-May as they move northward to their breeding grounds in Alaska (Lewis et al. 2007). This timing typically coincides with the spawning of the Cherry Point stock in mid-April through early May. Anecdotally, Surf Scoters have been observed in large numbers feeding on eggs and are thought to be a major source of egg mortality at the Cherry Point spawning site. This elevated predation of Surf Scoters on herring eggs has not been observed at other spawning sites and has been identified as an important area for future research for this population (Shelton et al. 2014, The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018).

While bird predation has been documented, there has been little effort to understand other sources of egg predation in the Salish Sea, a topic which might be beneficial for the understanding the lack of recovery in depressed populations. Unlike highly visible, surface-oriented birds, in-water predators such as fish and invertebrates are much more difficult to study without highly invasive and/or labor-intensive methods, such as seining and scuba diving surveys. Because of this, few studies have been conducted to understand the role fish and invertebrates have as predators for Pacific Herring eggs. In the early 1990s, invertebrate predation was estimated by diver surveys and lab studies, but the results were highly variable between sites. One study found invertebrate predation accounted for 1-30% of egg loss and another study found between 4-13% in the Strait of Georgia (Haegele and Schweigert 1990, Haegele 1993). Only one study has been conducted on fish predation, finding that just two species of greenling consumed between

2.3-3.7% of herring eggs on Montague Island in Prince William Sound (Rooper and Haldorson 1999). More studies have been conducted on Atlantic Herring eggs, finding that during low-density spawn events, fish predation made up to 40-60% of egg loss (Johannessen 1980). A variety of fish species (e.g., sandeels, perch, and haddock) were found to be important predators on Atlantic Herring eggs (Rankine and Morrison 1989, Toresen 1991, Rajasilta et al. 1993). It's important to note that these estimates were collected by seine or diver surveys and are snapshots in time; therefore, they may not account for turnover of fish moving in and out of the spawn area. More recent studies have used stable isotope analyses and identified spawning events as having significant bottom-up influences on the nearshore invertebrate community (Fox et al. 2018). The high variability in fish and invertebrate predation could be driven by egg availability (i.e., variation in spawning time), but also by habitat type, availability of alternative prey, and environmental conditions.

The Cherry Point stock could be experiencing more predation than other stocks due to its unique late spawning time. While studies have shown that the Cherry Point stock's spawn timing coincides with the timing of scoter migrations through the Salish Sea, there are other seasonal effects at play. For example, species richness in nearshore fishes generally increases between May and June in this region coincident with warming surface waters (Rice et al. 2012). Shiner Perch (*Cymatogaster aggregate*), an abundant nearshore fish, have been documented to switch diets from zooplankton to benthic organisms and fish eggs during periods of low plankton abundance in winter and early spring months (Odenweller 1975). Understanding how nearshore fish and invertebrates consume herring spawn is important in understanding recruitment variability in the Cherry Point population, as well as in herring and nearshore spawning forage fishes more broadly.

The population decline of the Cherry Point stock, a vital forage fish in the Salish Sea, will likely have cascading effects on ecosystem dynamics in our local waters. To address concerns regarding their recruitment success, I conducted an exclusion experiment to quantify egg loss during the incubation phase. The primary objective was to determine whether avian predation has a significant impact on

Pacific Herring recruitment at the current Cherry Point spawning site. Another hypothesis in need of research is whether the Cherry Point stock is experiencing increased predation from the nearshore fish, bird, and invertebrate community due to its late spawn timing and spawning behavior. To that end, I deployed remote underwater time lapse cameras at spawning locations of both the declining Cherry Point stock and a nearby stock with stable population trends (Semiahmoo Bay) to determine whether large fish and invertebrates in the nearshore, shallow-water assemblage are aggregating at the time of spawning. I hypothesized that organisms in addition to birds are utilizing Pacific Herring spawn as a pulse resource, defined as an event of increased resource availability with relatively high intensity, low frequency, and short overall duration (Willson and Womble 2006, Yang et al. 2010, Thomas et al. 2011).

This study aims to understand (1) whether the impact of predation has a significant effect on egg survival on the Cherry Point spawn, (2) how predation differs between Cherry Point and Semiahmoo Bay, and (3) if fish, birds, and invertebrates of the nearshore community aggregate at spawning sites and utilize Pacific Herring spawn as a pulse resource. These objectives directly address the lack of recovery in the Cherry Point stock and the ecological interactions between Pacific Herring eggs and the nearshore community to understand the impact of a declining population.

Methods

Study Site

The current spawning site is located along a southern facing shore (Birch Head) and is highly exposed to southerly winds, with a long fetch, creating an energetic wave environment during storm events (Figure 3). Unlike other herring stocks in the southern Salish Sea, Cherry Point herring have a shallow spawn depth ranging from 0-2 feet at Mean Lower Low Water (MLLW; Sandell et al. 2019). Spawning occurs in the rocky intertidal zone with patches of sand containing eelgrass (*Zostera marina*), red, and brown algae. The Cherry Point stock of Pacific Herring typically spawn on *Sargassum muticum*, an invasive brown alga, though small amounts of spawn have been seen on eelgrass and red algae. Eelgrass is present in the area but has not been used as the dominant spawning substrate in recent years (Sandell et al. 2019). We conducted predator exclusion experiments at the Birch Head study site from May 3-12, 2021 (first experiment), May 3-14, 2022 (second experiment), and May 20-30, 2022 (third experiment), coinciding with spawning events in 2021 and 2022. Remote underwater timelapse cameras were deployed from April 16-May 23, 2021, and April 18-June 6, 2022. HOBO Tidbit temperature sensors were deployed in the spawning location from May 1-23, 2021, and from May 19-June 6, 2022.

The Semiahmoo Bay stock spawning grounds overlap spatially, but not temporarily, with the Cherry Point stock (Sandell et al. 2019). Spawning typically occurs from January to March in Drayton Harbor and on a westward facing sandflat in a similar depth range as the Cherry Point stock but farther offshore due to the location of the sandflat. The dominant spawning substrate is *Zostera marina* and very little *Sargassum muticum* is found in the area. Remote underwater timelapse cameras were deployed from February 24-June 6, 2022, just offshore of the Semiahmoo Spit and north of Birch Head.

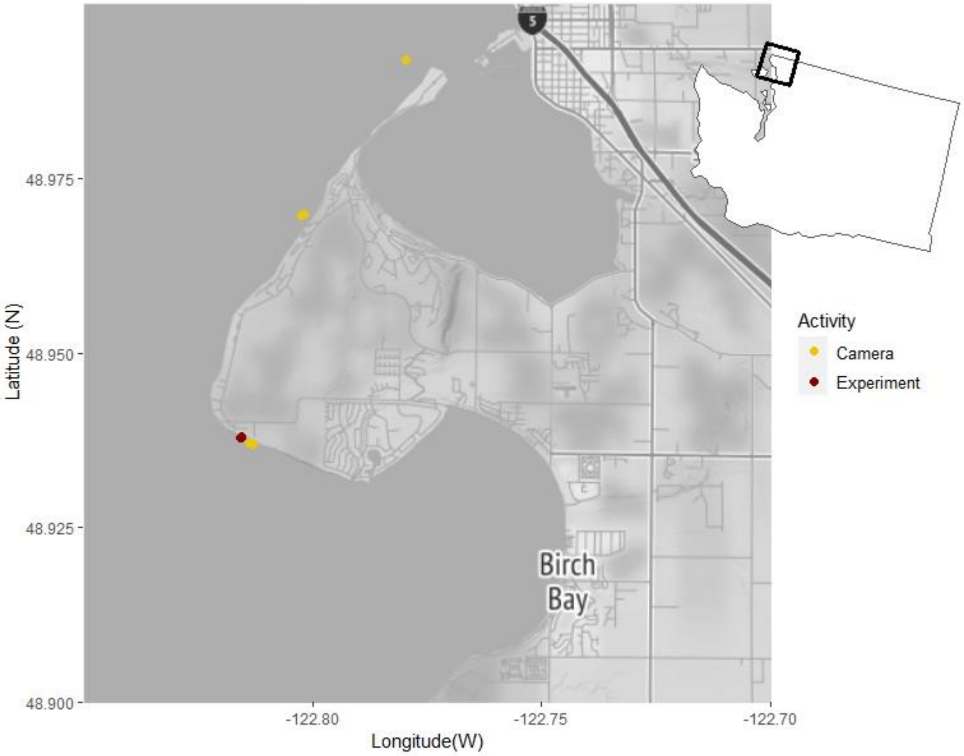

Figure 3: Site map of experiment (Cherry Point stock only) and camera deployment locations for the Cherry Point stock and Semiahmoo Bay stock spawning events. The Semiahmoo Bay stock spawns north of Birch Head along the Semiahmoo Spit and in Drayton Harbor in late winter and the Cherry Point stock spawns at Birch Head, typically in April and May.

Exclusion Experiment

Field

Predator exclusion experiments were conducted by establishing control and exclusion plots in the spawning area at peak spawn abundance. Recent spawning activity was identified by WDFW aquatic vegetation rake surveys and beach walks in the intertidal zone. Once herring spawn was observed in a suitable location for the experiment, exclusion and control plots were deployed in the area, typically within 48 hours of reports of spawn. Three commercial sablefish pots (0.41m height, 0.74m diameter) were retrofitted with 1-3/4” (7/8” square) stretch mesh webbing and haphazardly placed over eggs, to avoid large boulders. The pots functioned as exclusion treatments to make eggs inaccessible to avian predators, large fish, and large crabs (Figure 4). Control plots had no excluder but were a defined area demarcated by lead line (staked into the substrate) for sampling repeatability. The control plots were located at one end of the spawning area, slightly separated from the cages, to minimize any effect the cages could have on foraging activities.

Over the approximately two-week egg incubation period, vegetation inside each plot was repeatedly sampled. To obtain a representative sample of egg density within each plot, three samples were taken from high, medium, and low-density areas in the plot. These subsamples were collected by SCUBA diving if the eggs were more than 4 ft underwater and by snorkeling or wading if accessible at lower tides. The eggs from these subsamples were put into Ziplock bags underwater, transferred to plastic bottles, and preserved in Stockard’s solution (Schweigert and Fournier 1982, Schweigert et al. 1985, Shelton et al. 2014) after our return to the laboratory. In conjunction with the sampling, snorkel surveys were conducted to estimate the percent cover of spawning substrate and the percent cover of eggs for each plot.

During the time of the experiment in 2021, our collaborators from WDFW conducted bird surveys to determine surf scoter abundance in the vicinity of the experiment; bird surveys were not conducted in 2022. In 2021, bird surveys were conducted in 3 geographical areas: north of Birch Head, Birch Head south to Point Whitehorn, and south of Point Whitehorn, for 3 days of each week from April

14 – May 13th. This time period was chosen to identify relative bird abundance pre-spawn, during incubation, and post-spawn within the year. Full methods are available in Dionne et al. 2022.

Figure 4: Retrofitted sablefish pot used as exclusion treatment at Birch Head spawning area.

Laboratory

All collected eggs were removed from spawning substrate and counted under a dissecting scope so surface area of the algae could be measured according to the methods of Shelton et al. 2014 (Figure 5). In the third experiment, I assessed egg viability. Eggs with opaque flesh or yolk and/or a non-distinct body outline were identified as nonviable (Bishop and Green 2001). Approximate surface area of the spawning substrate (*Sargassum muticum*) was obtained by measuring the diameter of the algal stipes (d) and the length of the algae (l, Equation 1). From the egg counts and surface area calculations I obtained the approximate egg surface density in each plot on each sampling day. This method allowed me to determine egg abundances for each sampling event over the two-week period, mortality during this period, and differences between the treatments and the controls to quantify the impact of predation on egg survival.

$$SA = \pi d l \qquad \text{Equation 1}$$

Figure 5: Pacific Herring eggs collected in spring 2022 from the Cherry Point stock under a dissecting microscope. Eyes are visible and the embryos have at least one tail wrap, indicating they are roughly 11 days old.

Remote Underwater Time-lapse Cameras

Remote cameras were deployed approximately two-weeks before the predicted spawning event, throughout the egg incubation period, and approximately one-week post larval transition to understand how the nearshore community changed with the presence of spawn. I used Afidus ATL - 200S cameras, which are a programmable time-lapse camera that are specifically designed to be left outside for long durations (weeks to months) with minimal maintenance. To extend the battery capacity of the camera, Voltaic V50 external power banks were used to run the cameras. The camera and power bank were duct taped inside a clear Plano waterproof case that was mounted with rubber ski straps to t-posts driven into the substrate (Figure 6). Pre-spawn deployment of the cameras were in locations close to historical spawning sites provided by WDFW. Once spawning took place, the cameras were moved as close as possible to the spawn while still being accessible at low tide to change batteries and memory cards. With external power banks and a 64 GB memory card the cameras could be left unattended and take a photo every 5 seconds from 6:00-20:00 every day (daylight hours) for approximately 6 days, yielding a total of approximately 10,080 images/day.

Figure 6: Remote underwater timelapse camera deployed in an eelgrass bed in Semiahmoo, WA.

The photos were edited into a time-lapse video which could be paused and reviewed frame by frame. The time-lapse videos were reviewed and screenshots with date and time were taken of all organisms captured in the footage. The screenshot images were first reviewed by undergraduate interns who identified organisms to the lowest taxonomic level possible; I further reviewed all positive images to verify identification and abundance. We recorded the maximum number of individuals (MaxN) for each species that appeared at any one time in a 30-minute interval, to avoid double counting individuals, as an index for relative abundance (Dunlop et al. 2015, Aguzzi et al. 2020). All data were binned into 30-minute intervals and recorded in spreadsheets.

Analysis

All data transformation and statistical analyses were conducted in the R programming environment (v4.0.4; R Studio Team 2021). Generalized linear models (GZLM) were used to compare the surface density of eggs (count/cm^2 of substrate) during the field experiment by treatment type (control and excluder), day of the experiment, and experiment number (first, second, third, corresponding to the 2021 and two 2022 experiments). A linear model (Equation 2) represents the linear relationship between a response variable (Y) and an explanatory variable (X_i). The intercept is represented as β_0, β_i corresponds to the coefficient for each explanatory variable and ϵ is the error term. Because the relationship between egg density and the explanatory variables is unknown (and perhaps not linear) and density from counts is lognormally distributed, I used a negative binomial GZLM with a logarithmic link function to ensure the fitted values were non-negative (Zuur et al. 2009). These models were used to identify which of the explanatory variables had a significant effect on egg surface density through the incubation period and to determine the strength of the effect size. The primary explanatory variable was treatment type (control or excluder), but I was also interested in whether individual experiments differed from each other (first, second, third). Day of experiment was included to address egg mortality over time. Summary statistics and plots were used to demonstrate percent cover of eggs and egg viability over the incubation period.

$$Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_p X_p + \epsilon \qquad \text{Equation 2}$$

Non-metric multidimensional scaling (nMDS) analysis is a robust approach for looking at patterns in community datasets, taking into account species richness and abundance of individual species. Non-metric multidimensional scaling is a subcategory of multidimensional scaling that finds a non-parametric relationship between the dissimilarities among a group of points. The analysis starts by randomly placing data points in space and then computing the stress, which is the difference between the data point's original dissimilarities and their dissimilarities in reduced dimensional space. Next, an iterative algorithm is used to find the mapping of the data points that minimizes the stress (or distance among all points). The stress is defined by an equation (Equation 3) where the d_{ij} term represents the actual dissimilarity between samples and the $\tilde{d}_{ij}$ term represents the fitted dissimilarity. Stress is used as a metric to indicate how well the algorithm has optimized the data points in multidimensional space and as a guideline for the interpretation of the ordination. For instance, with a stress of less than 0.05, the ordination gives an excellent interpretation of the data. With a stress of less than 0.1, the ordination gives a good interpretation and with less than 0.2 it gives an acceptable interpretation (Dexter et al. 2018). According to most guidelines, a stress of higher than 0.2 gives a poor interpretation. It's important to note that recent studies have pushed back against these strict guidelines, especially for larger datasets (n > 100), as the stress guidelines were developed with small datasets in mind (Dexter et al. 2018).

$$Stress = \frac{\sum_{ij}(d_{ij}-\tilde{d}_{ij})^2}{\sum_{ij} d_{ij}^2} \qquad \text{Equation 3}$$

The timelapse camera data were prepared for nMDS analysis by first grouping the 30-min time chunks into larger time-of-day intervals. Four time-of-day intervals were selected based on previous knowledge of fish activity and the duration of measurements: 6:00-9:00 for the "Morning," 9:30-12:30 for the "Mid-morning," 13:00-16:00 for the "Mid-afternoon," and 16:30-19:30 for the "Evening" interval. The sum of the MaxN for each of the ten most abundant species (from both years) was calculated by the date and the time-of-day interval. Observations with all zeros were removed from the dataset to make the estimation more efficient. The MaxN data were then transformed using a square root transformation, to reduce skewedness in the data distribution. I used the *metaMDS* function of the Vegan package with the Bray-Curtis dissimilarity measure (best measure for count data) and the default auto transformation for a community dataset (Wisconsin double standardization, McGlinn et al. 2020). I used a minimum of 1000 random starts in search of a stable solution and a maximum of 1000 iterations in a single run to prevent local minima. Three dimensions was the maximum used in the analysis because interpreting the results gets significantly harder with more than three dimensions. The results from the nMDS analysis were visualized with scatter plots that included the prediction variables of spawn period (pre-spawn, spawn, post-spawn) and year (2021-2022), to assess variability in assemblage.

The *Envfit* function of the Vegan package was used to run free permutations to assess the significance and goodness-of-fit for each fitted predictor variable, spawning period type (pre-spawn, spawn, and post spawn) and year (McGlinn et al. 2020). Further analysis was done with the *Adonis* function of the Vegan package which performs a permutational multivariate analysis of variance using distance matrices (Anderson 2017, McGlinn et al. 2020). PERMANOVA analysis is used to compare groups of objects by testing whether the centroids and the dispersion of these groups are equal (Anderson 2017). I used *betadisper* to test for multivariate homogeneity, which is an assumption of the PERMANOVA analysis (McGlinn et al. 2020). Once multivariate homogeneity of variance was confirmed, I performed a PERMANOVA analyses on the species communities to assess differences in the spawn period type (pre-spawn, spawn, post-spawn) and sampling year.

Environmental data were summarized with plots. I described temperature change across the sampling period from the temperature logger data and related fish abundance with temperature and tidal height.

Results

Three waves of spawning occurred from Spring 2021-Summer 2022 and predator exclusion experiments were set during each wave of spawn. The 2021 spawning event (first experiment) occurred closest to Birch Point and the 2022 events (second and third experiments) occurred approximately 250 m southeast of this location; both 2022 events were in the same location several weeks apart. The spatial extent of each wave of spawn was similar, with an average coverage area of 150 m^2. Egg density in the first and second experiments was similar throughout the incubation period, but the third experiment had a starting egg density of more than double the previous experiments (Figure 7).

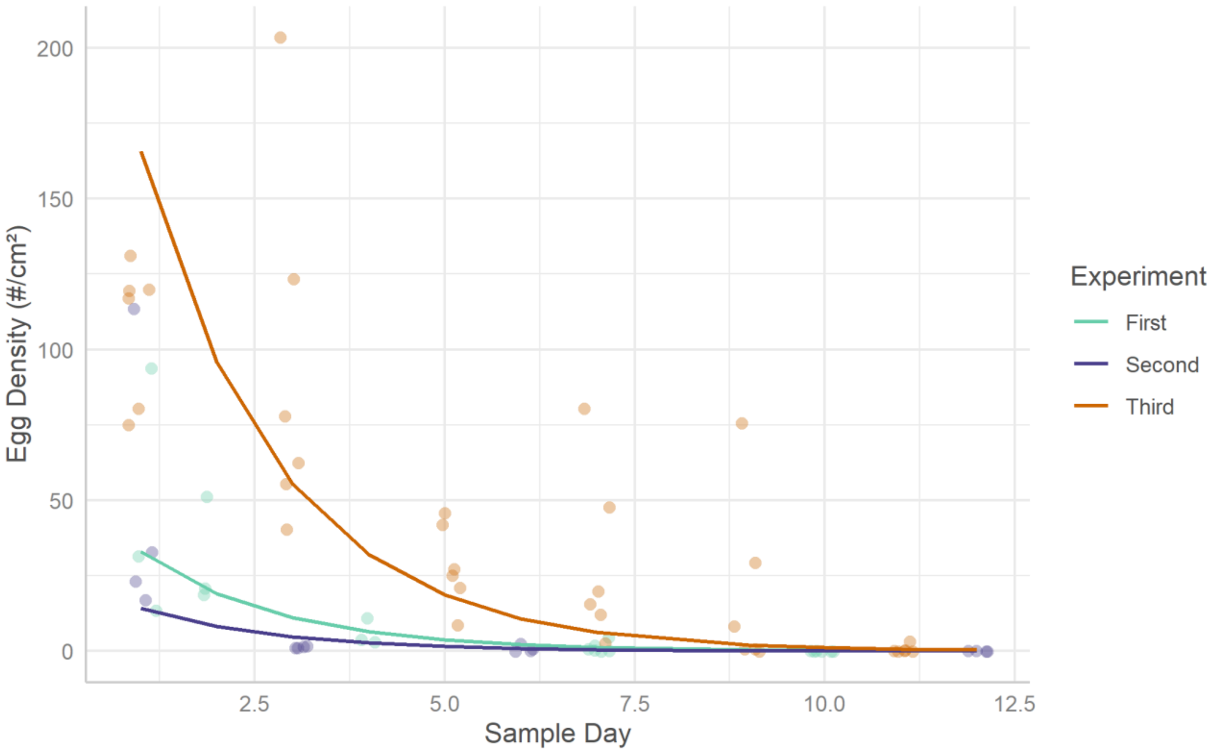

Figure 7: Pacific Herring egg density (egg count per cm^2) throughout the incubation period. Color represents each experiment that was deployed during spawn events. First experiment (light green) deployed in early May 2021, second experiment (purple) deployed in early May 2022 and third experiment (orange) deployed in late May 2022. Day refers to the day of sampling (n) through the time of deployment (replicate counts for each day). Outliers were checked with residual plots and retained for analysis. Fitted lines represent a negative binomial generalized linear model (Density~Day).

Surf scoters were the most abundant bird species observed in the sampling area during the 2021 experiment with relative abundances building from April 14-16th (Pre-spawn), peaking from April 20-29th (Pre-spawn), and rapidly declining May 4-13th (Spawn, Dionne et al. 2022). The bird surveys indicate that avian abundance was highest before spawning occurred and that most birds had left the spawning area before or during the incubation period. Surf scoters were concentrated off Birch Head, consistent with where spawn was observed; however, due to spawn timing only very early spawns (which were not observed by spawn surveys in 2021 but may have gone undetected) would have been vulnerable to surf scoter predation. More detailed bird survey results are provided in Dionne et al. 2022.

Exclusion Experiment

Percent cover estimates are only reported for the first and third experiments because significant wave activity prevented us from obtaining accurate estimates for the entirety of the second experiment. A comparison between experiments showed that the third experiment had significantly slower rates of decline in percent egg cover over the course of the incubation period than the first experiment ($p < 0.001$; Figure 8). When I compared rates of decline for percent cover between treatment types within experiments, the third experiment showed a significant difference in the intercepts of treatment groups ($p < 0.001$) and the first experiment showed no difference between treatment groups ($p < 0.878$; Figure 9).

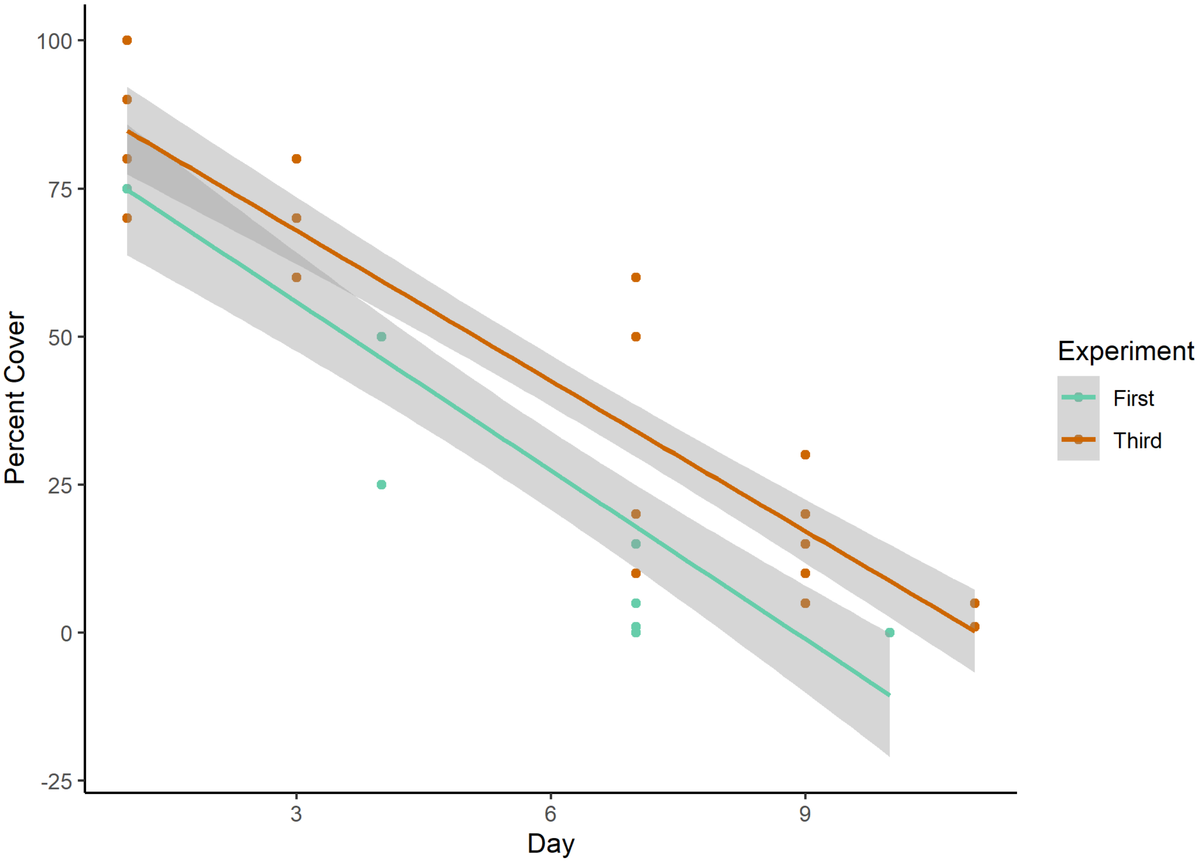

Figure 8: Percent cover of Pacific Herring eggs for the first experiment (light green) in early May 2021 and third experiment (orange) in late May 2022. Percent cover includes data from both the control and exclusion plots for each experiment. Fitted lines represent a linear regression with gray bands indicating 95% confidence intervals.

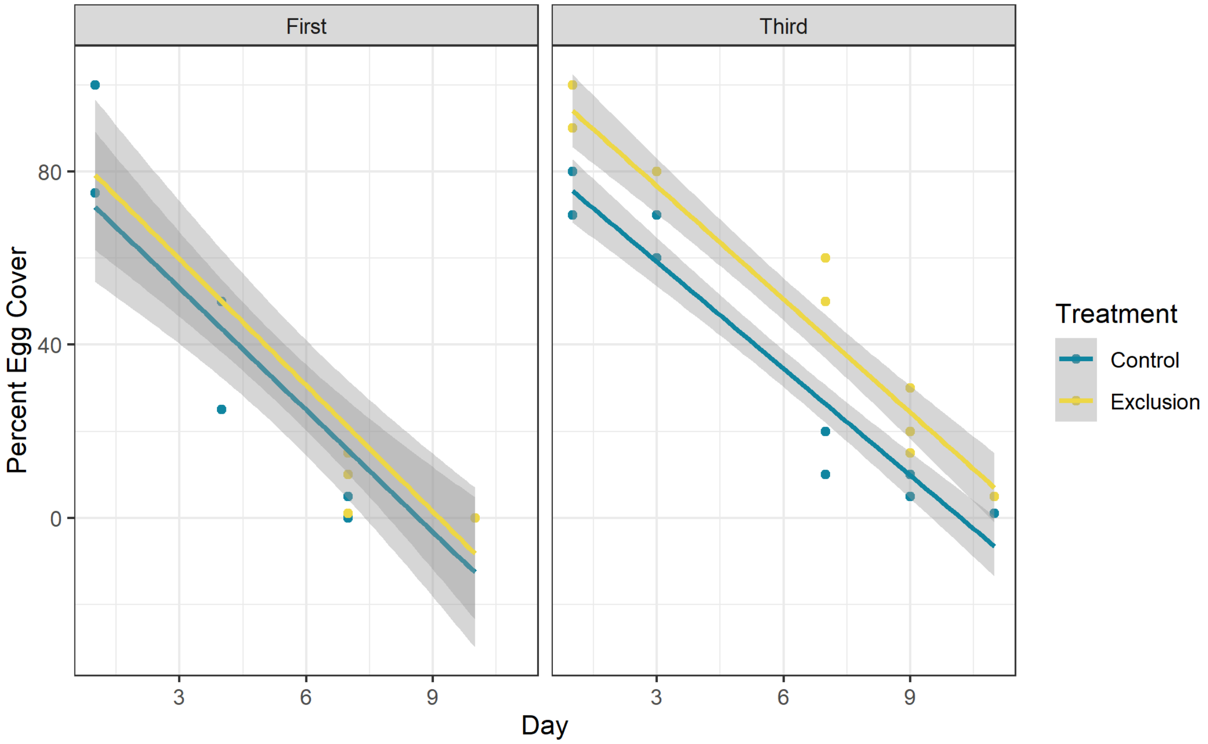

Figure 9: Percent cover of Pacific Herring eggs throughout the incubation period for the first experiment in May 2021 and the third experiment in late May 2022. Color represents percent cover from control (blue) and exclusion (yellow) plots. Fitted lines represent a linear regression with gray bands indicating 95% confidence intervals.

A negative binomial generalized linear model was used to describe the egg density from the predator exclusion experiment. The best fitting model, determined with Akaike Information Criterion (AIC) scores, included experiment (First, Second and Third), treatment type (Control and Excluder), and the sample day (n). This model showed that the treatment type did not significantly affect the density of eggs (p-value = 0.711). When all three experiments were combined and examined by treatment type, similar egg loss was observed between those eggs exposed to avian, large fish, and invertebrate predation and those that excluded these taxa (Figure 10). While no significant differences were found between treatments, higher variability in egg density was found in the exclusion plots compared to the control plots for each experiment (Figure 11).

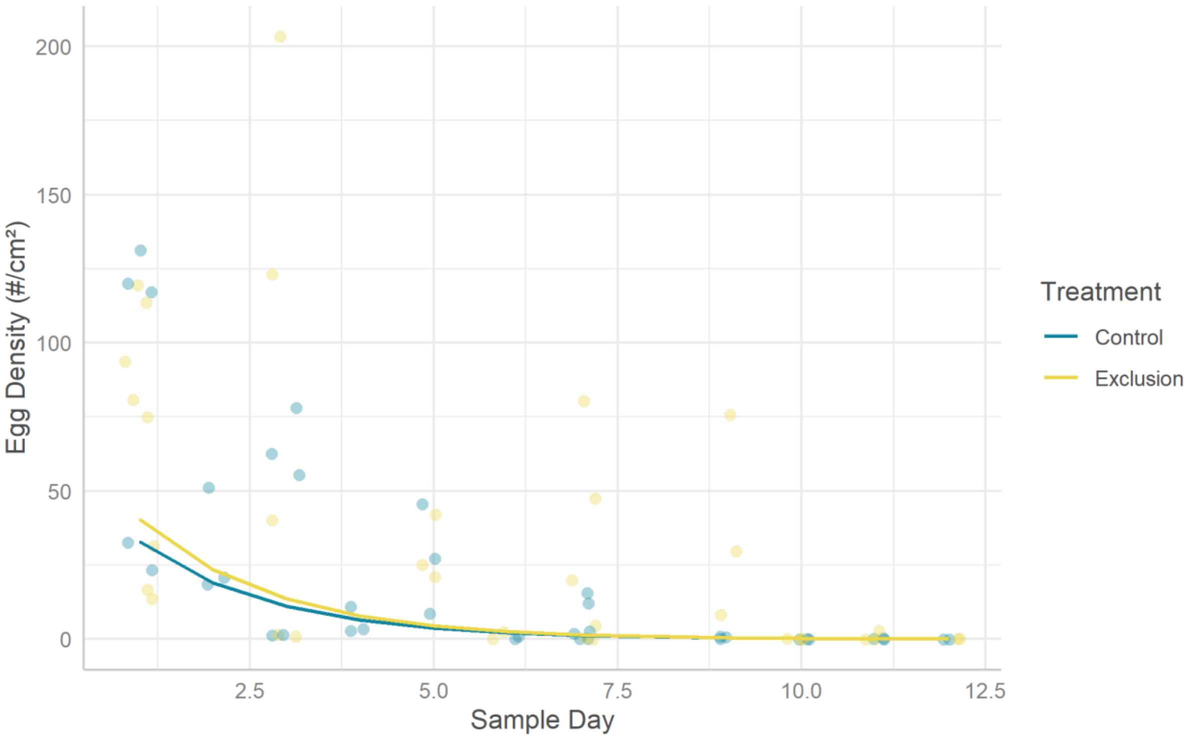

Figure 10: Pacific Herring egg total density (egg count per cm^2) throughout the incubation period. Data is combined for all three experiments and grouped by treatment type. Color represents density from control (blue) and exclusion (yellow) plots. Outliers were checked with residual plots and retained for model fitting. Fitted lines represent a negative binomial generalized linear model (Density~Day).

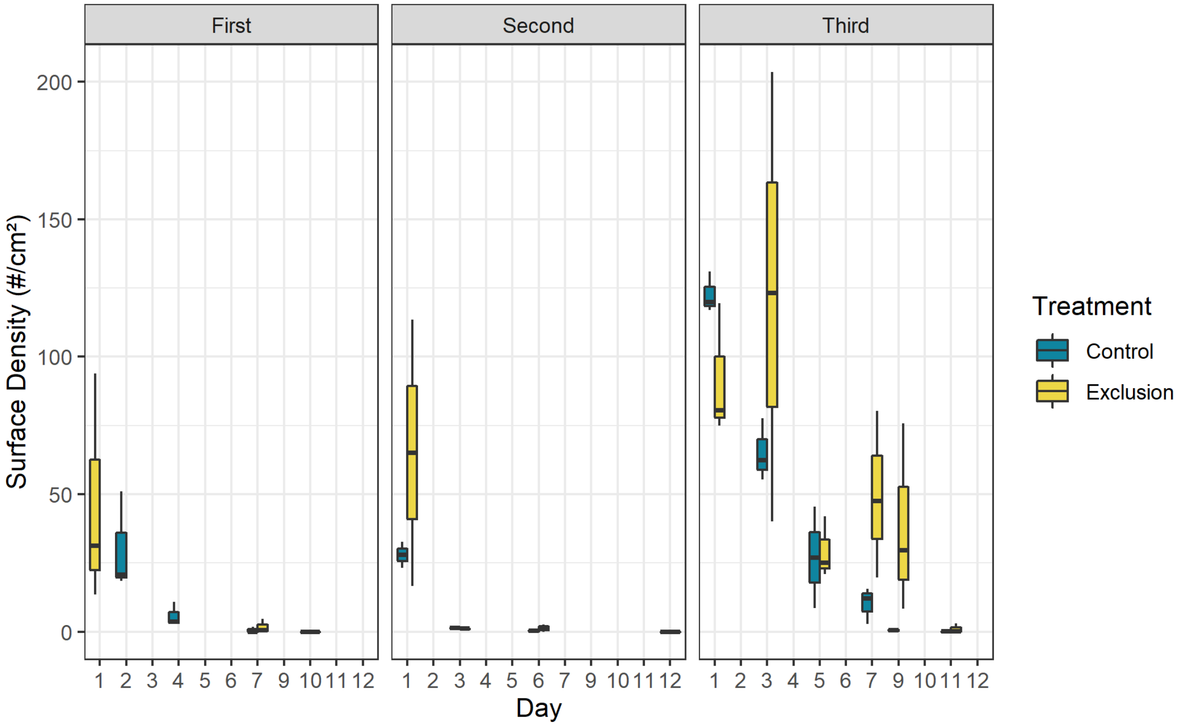

Figure 11: Boxplots depicting egg densities (egg count per cm^2) throughout the incubation period for each experiment deployed. Colors represent the treatment type.

By analyzing the three experiments separately, I found that the third experiment had a starting egg density of more than double the two previous experiments (Figure 12). A generalized linear model found a significant difference in egg density between the third experiment and the previous two (p-value < 0.001).

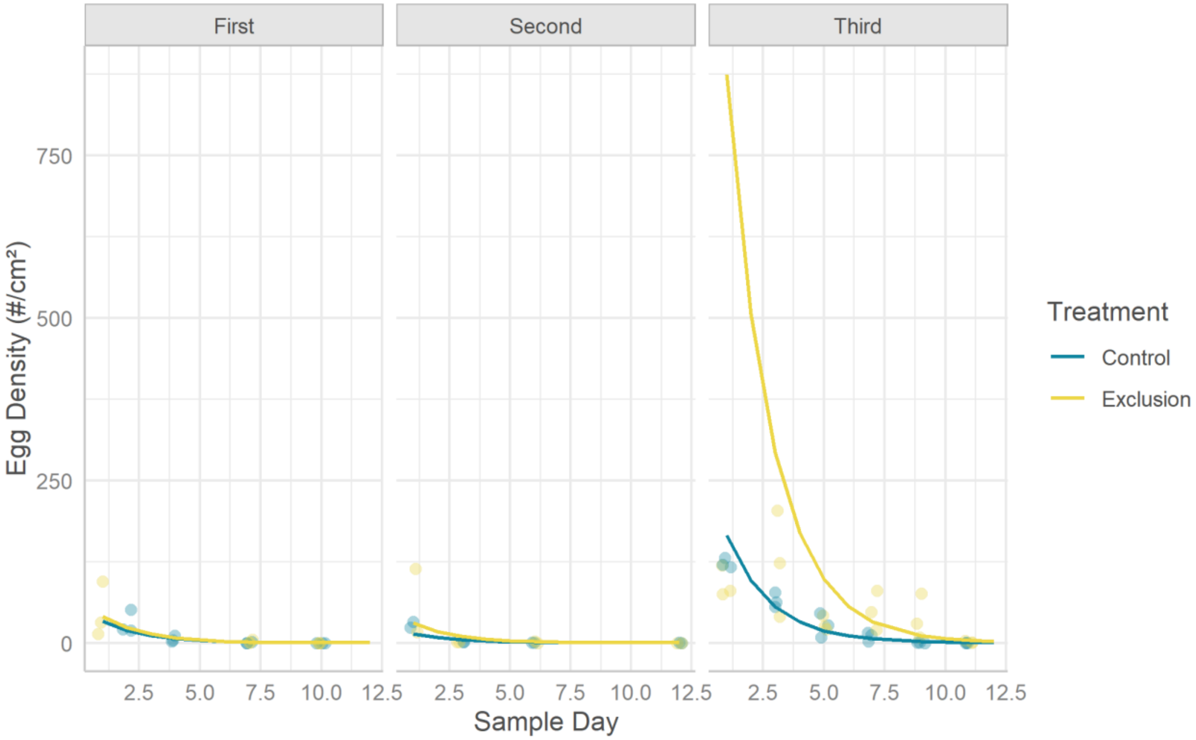

Figure 12: Pacific Herring egg density (egg count per cm^2) throughout the incubation period for each experiment that was deployed. Colors represent the two treatment types, control (blue) which were plots open to predation and exclusion (yellow) which were plots excluding large predators from accessing eggs. Fitted lines represent a negative binomial generalized linear model (Density~Day).

The proportion of non-viable eggs in both treatment groups was low, with approximately 90% of the eggs viable throughout the incubation period. Control plots showed a higher percentage of unviable eggs compared to exclusion plots ($t = 2.63$, $df = 11.94$, p-value $= 0.022$). The exclusion plots had an average of 2.8% unviable eggs throughout the incubation period whereas the control plots had an average of 8.6% unviable eggs (Table 1). The rate of unviable eggs in the exclusion plots stayed mostly constant throughout the incubation period unlike the control plots which varied more between sample days.

Table 1: Average percent of unviable Pacific Herring eggs from the third experiment during the spawning event in late May 2022.

Sampling Date	**Treatment**	**Average Percent Unviable**
5/22/2022	Control	6.4%
	Exclusion	2.0%
5/24/2022	Control	10.6%
	Exclusion	3.2%
5/26/2022	Control	8.7%
	Exclusion	2.6%
5/28/2022	Control	0%
	Exclusion	3.3%

Remote Underwater Timelapse Cameras

Remote underwater timelapse cameras were deployed from April 16-May 23, 2021, and April 18-June 6, 2022, at the Cherry Point spawning site and at the Semiahmoo site from February 24-June 6, 2022. Fish and bird indices of abundance were collected with timelapse cameras before, during, and after spawning periods for two sampling years and three spawning events. I identified 3 bird species, 15 fish species, 7 invertebrate species and 1 marine mammal (Table 2). The top ten numerically abundant species from both years, including unidentified (UID) fish and birds, were included in summary plots and statistical analyses.

Table 2: All species observed with the time-lapse camera for both years and stocks. Bolded text indicates the top ten most abundant species that were used in the analysis.

Fish	**Birds**	**Marine Mammals**	**Invertebrates**
Platichthys stellatus	***Histrionicus histrionicus***	*Phoca vitulina*	*Pleurobrachia bachei*
Rhacochilus vacca	*Gavia immer*		*Clytia gregaria*
Cymatogaster aggregata	*Larus glaucescens*		*Aequorea victoria*

Aulorhynchus flavidus	**UID bird**		*Polyorchis penicellata*
Citharichthys stigmaeus			*Neoturris breviconis*
Squalus suckleyi			*Metacarcinus magister*
Myoxocephalus polyacanthocephalus			Pugettia spp.
Parophrys vetulus			*Melibe leonina*
Embiotoca lateralis			
Ammodytes hexapterus			
Clupea pallasii			
Hexagrammos stelleri			
Gasterosteus aculeatus			
Scorpaenichthys marmoratus			
Microgadus proximus			
Salmonidae spp.			
Embiotocidae spp.			
Sculpin spp.			
UID fish			

The Semiahmoo samples had lower species diversity and abundance as well as fewer observations during the spawn period compared to the Cherry Point samples (Figure 13). Most observations for the Semiahmoo stock occurred during the post-spawn period and were later in the season. When abundances through time were evaluated for just the Cherry Point stock, in 2021 there was a peak abundance during the incubation period followed by abundances decreasing from mid-May to late-May during the post-spawn period. I did not observe these trends in 2022, when abundances were variable but didn’t decline over time (Figure 14).

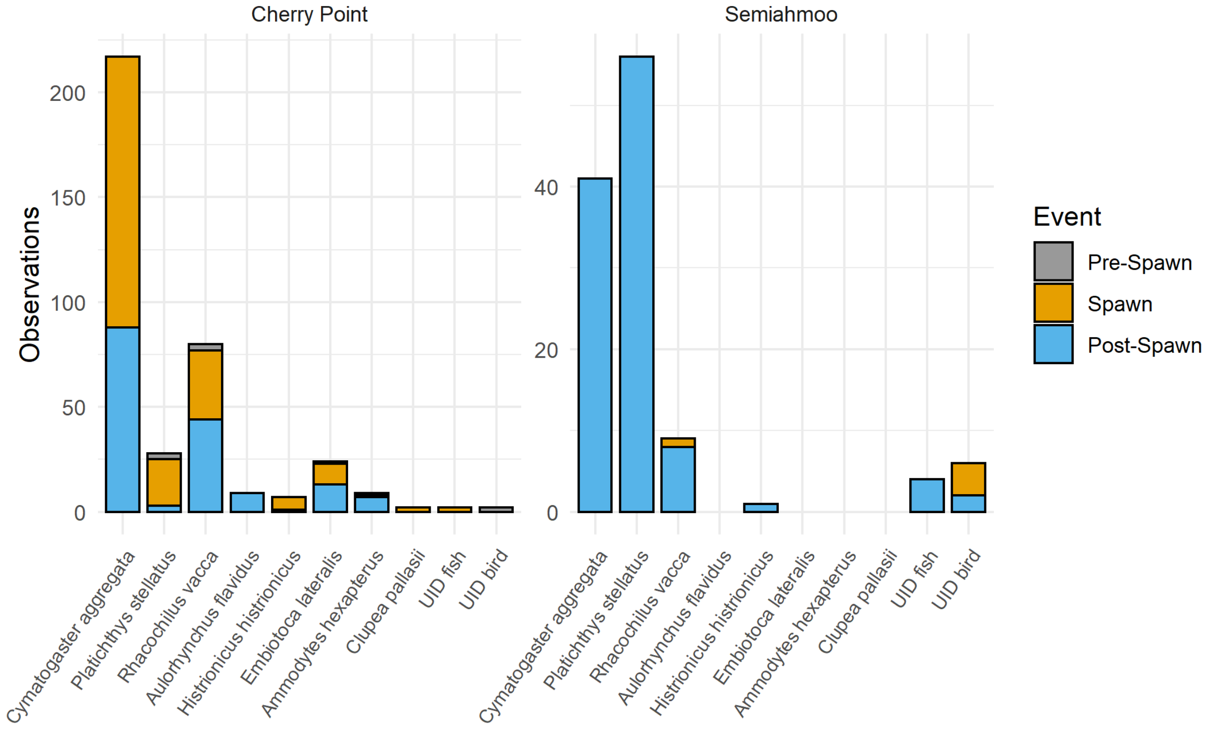

Figure 13: Frequency of occurrence for the top ten groups at the Cherry Point stock spawning event separated by stock. Color represents the spawn period. Data include the Cherry Point stock in 2021 and 2022 and the Semiahmoo stock in 2022.

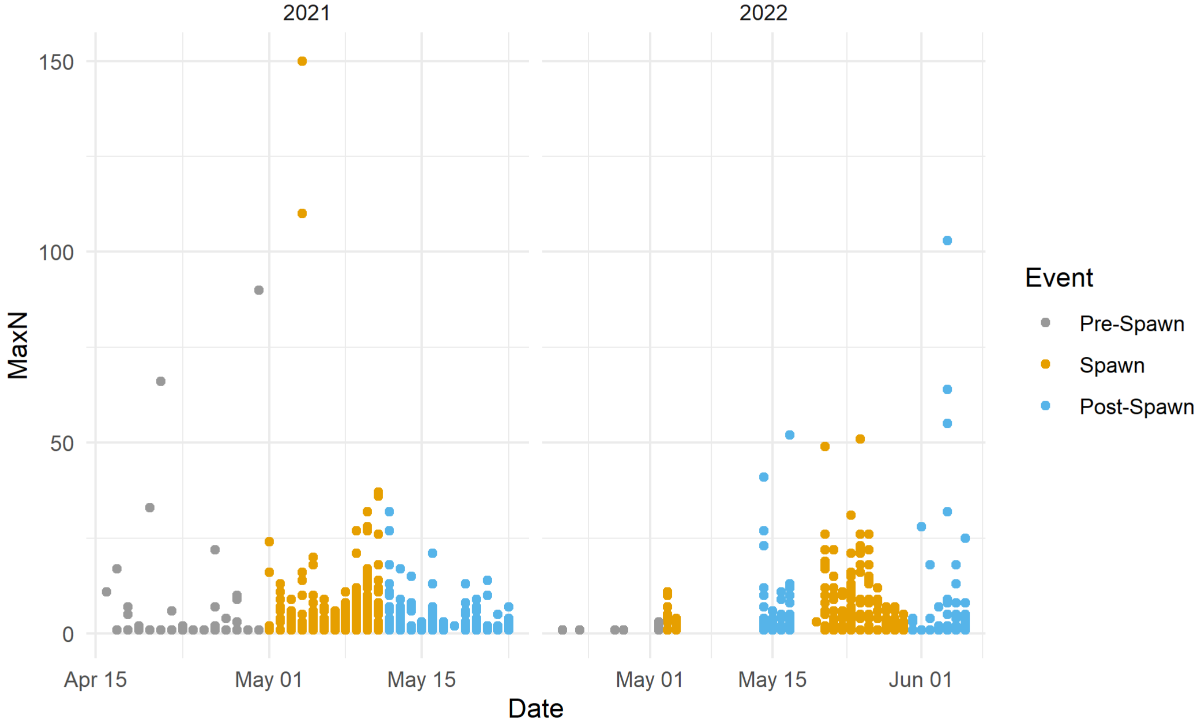

Figure 14: Scatter plot of MaxN (index of species abundance) at the Cherry Point stock through time for 2021 and 2022. Colors represent the spawning event type.

To determine if spawning attracted predators at the Cherry Point spawning area, I evaluated frequency of occurrence and abundance data obtained before, during, and after spawning periods and used these periods as categorical variables in the analysis. I observed large increases in the frequency of occurrence from the pre-spawn period to the spawn and post-spawn periods for most of the common groups. Shiner Perch and Pile Perch demonstrated the most dramatic change in abundance from pre-spawn to spawn period, followed by Starry Flounder (*Platichthys stellatus*). There is less change from the spawn to the post-spawn event for all groups except Starry Flounder and Harlequin duck, whose observed abundances decline dramatically after the egg to larval transition (post-spawn period). For the Cherry Point stock, of the top ten groups, seven species of fish and one bird species increased in abundance from pre-spawn to spawn period (Figure 15). Most of these species returned to pre-spawn abundances after herring eggs hatched, except for Shiner Perch (*Cymatogaster aggregate*) and Pile Perch (*Rhacochilus vacca)*, whose abundances remained high post-hatching (Figure 15). Abundances in the top ten groups differed from 2021 to 2022 but the increase in spawn and post-spawn period abundances compared to pre-spawn abundances persisted through both years (Figure 16).

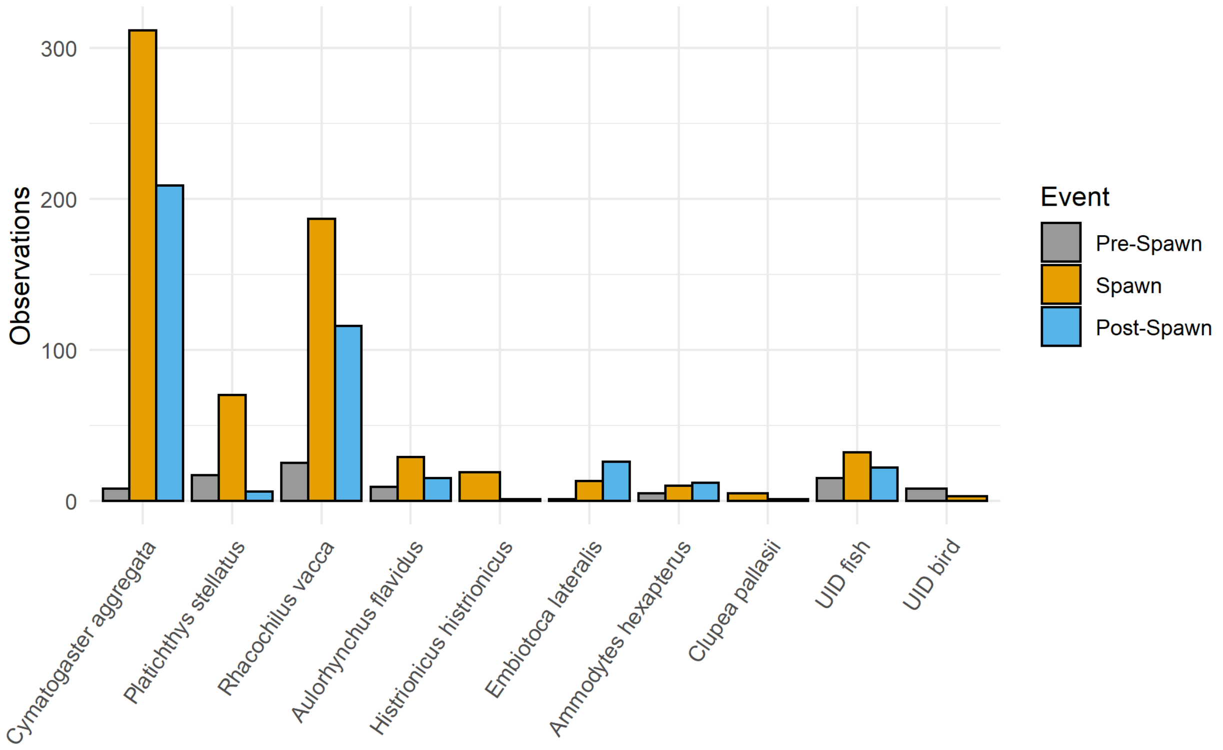

Figure 15: Frequency of occurrence for the top ten groups observed from the Cherry Point stock spawning periods in 2021 and 2022. Color represents the spawn period: pre-spawn (before spawning occurs) in grey, spawn (during incubation period) in orange, and post-spawn (after larval transition) in blue.

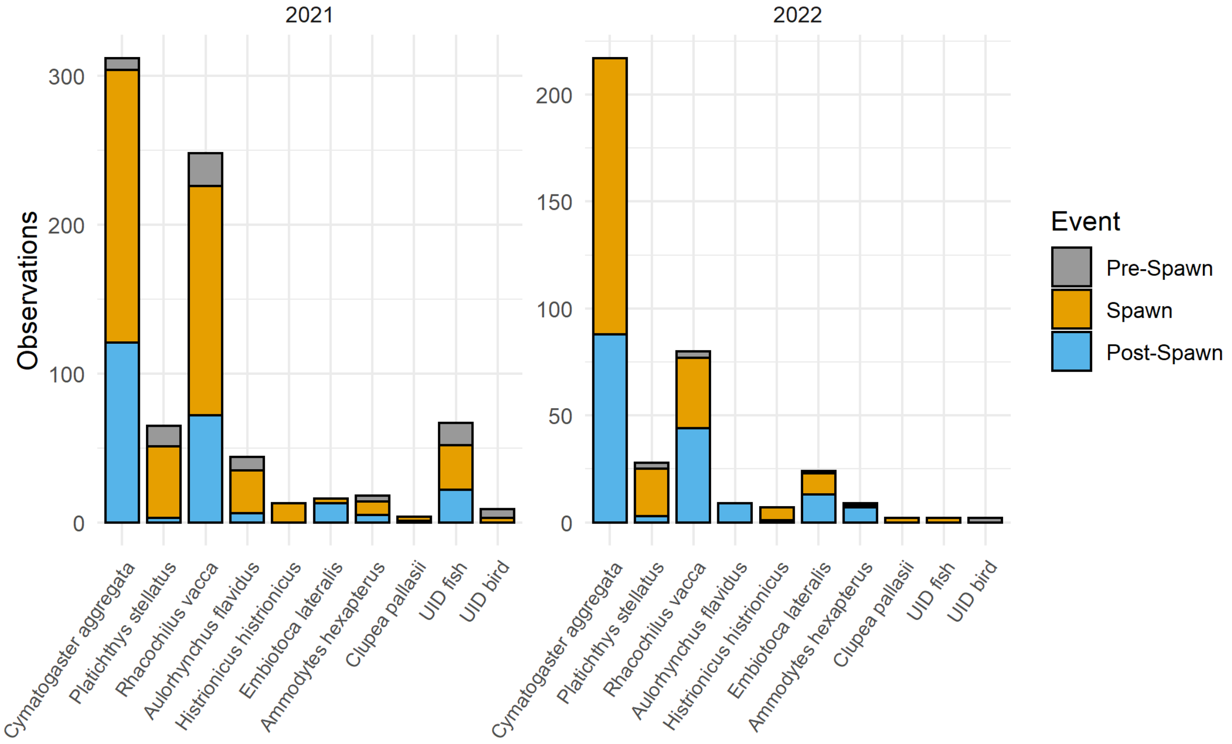

Figure 16: Frequency of occurrence for the top ten groups for the Cherry Point stock spawning periods separated by sampling year. Color represents the sampling period.

Non-metric multidimensional scaling analysis showed slight separation between pre-spawn predator communities and predator communities during (spawn) and after (post-spawn) the incubation period (Figure 17). The nMDS showed predator communities during and after the incubation period to be overlapping (Figure 17). A PERMANOVA analysis showed that there was a significant difference in assemblage (top ten species groups used above) among the spawn periods. However, period is not a significant predictor of the community composition, as it only explains about 17% of the variation in the dataset ($F_{(2,210)} = 22.874$, $r^2 = 0.172$, p-value = 0.001). Next, I looked at potential differences between years in predator assemblage and I found some separation between the sampling years using nMDS (Figure 18). PERMANOVA confirmed there was a significant difference in community composition by year ($F_{(1,210)} = 7.298$, $r^2 = 0.0274$, p = 0.001) but it was a very poor predictor and only explained about 3% of the variation.

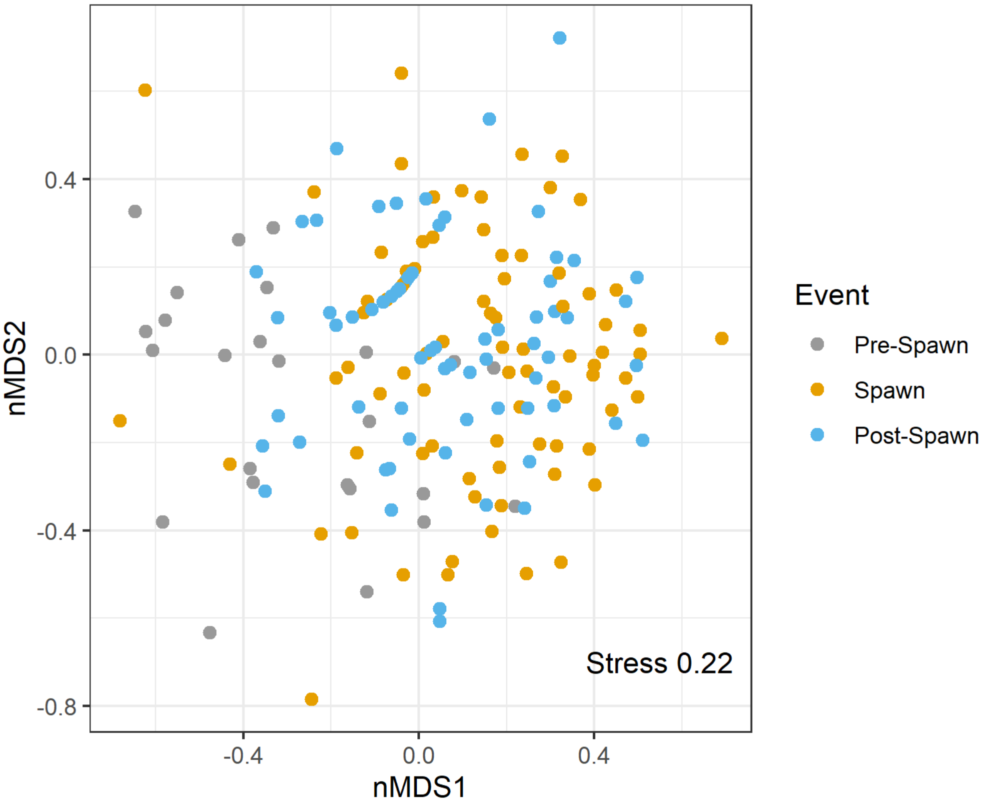

Figure 17: Scatter plot of a nMDS analysis (k =2) of the top ten predator groups. Colors represent spawn event type.

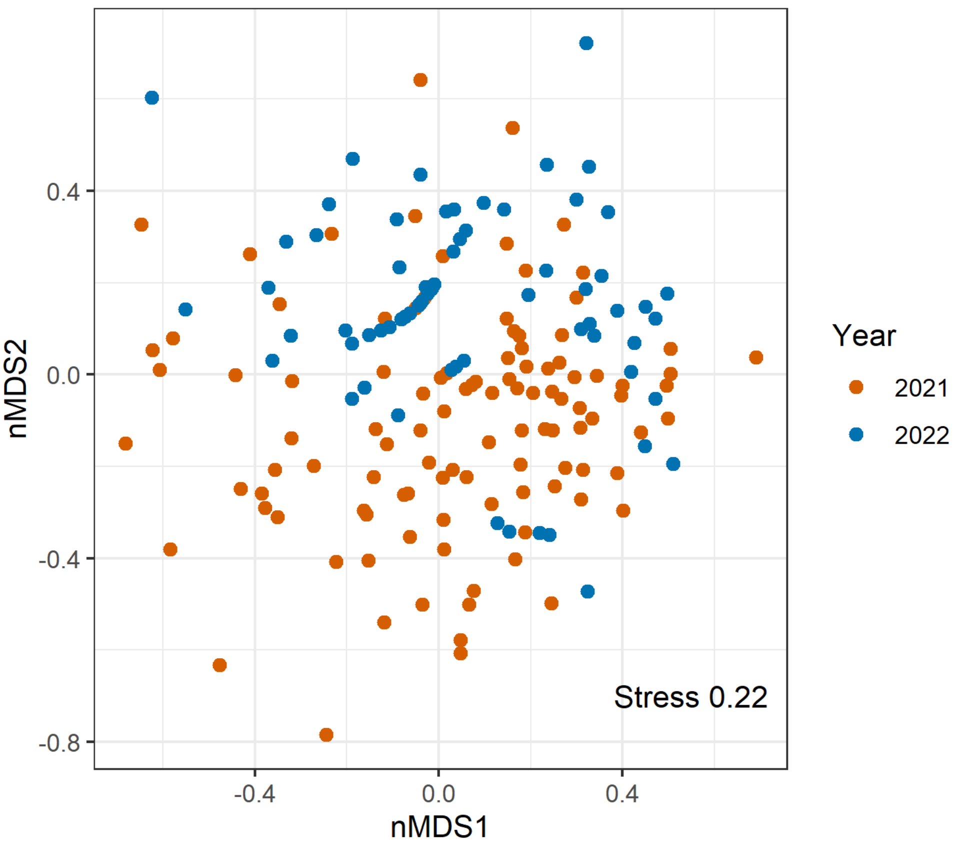

Figure 18: Scatter plot of a nMDS analysis (k =2) of the top ten predator groups. Color represents sampling year.

Environmental Variables

HOBO Tidbit temperature sensors were deployed at the Cherry Point site from May 1-23, 2021, and from May 19-June 6, 2022. To understand how environmental variables such as tide and temperature effect nearshore assemblages, I investigated whether observed species abundances (from time-lapse camera data) changed with these variables. When tidal height and predator abundances (MaxN) were plotted against each other, tide had very little correlation with the abundance of predators in the nearshore and for this reason was excluded from further analysis (Figure 19). I also evaluated the role of time of day in determining predator abundances (some species are known to be crepuscular feeders) and observed that early morning (6:00-8:00) and early evening (18:00 – 19:00) had the highest predator abundances regardless of tidal height (Figure 20).

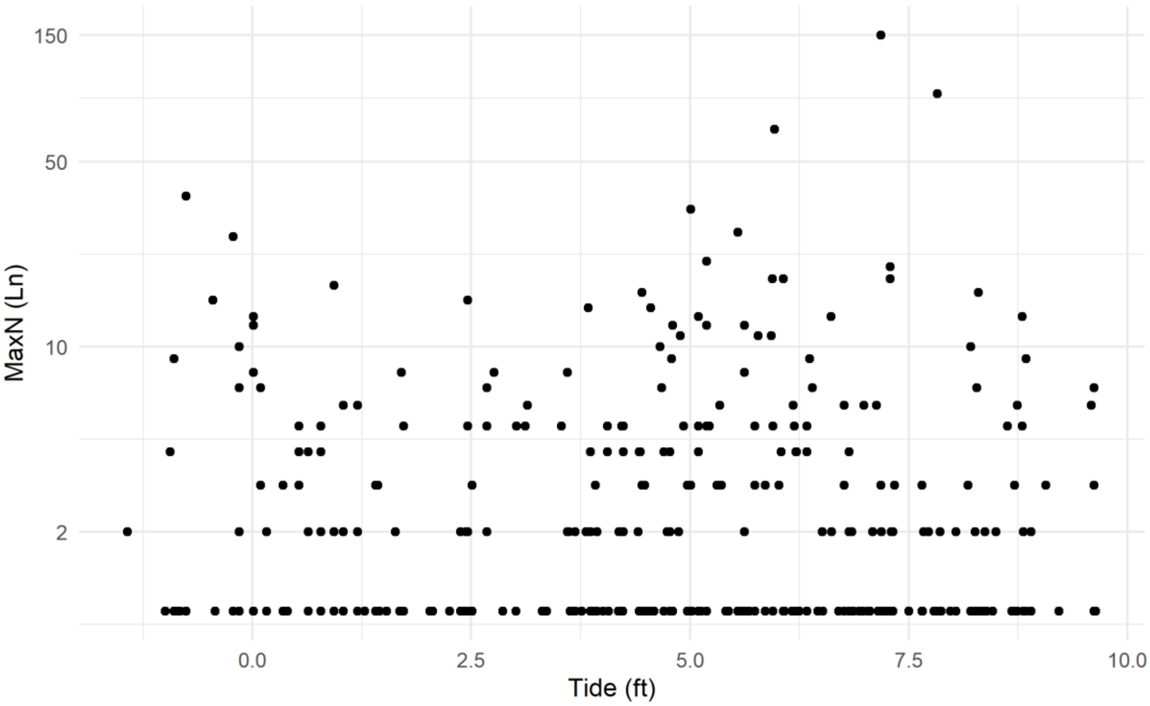

Figure 19: Tidal height in feet plotted against the index of relative abundance (MaxN) of predators. Abundance was set on a natural log scale to better assess patterns in the data.

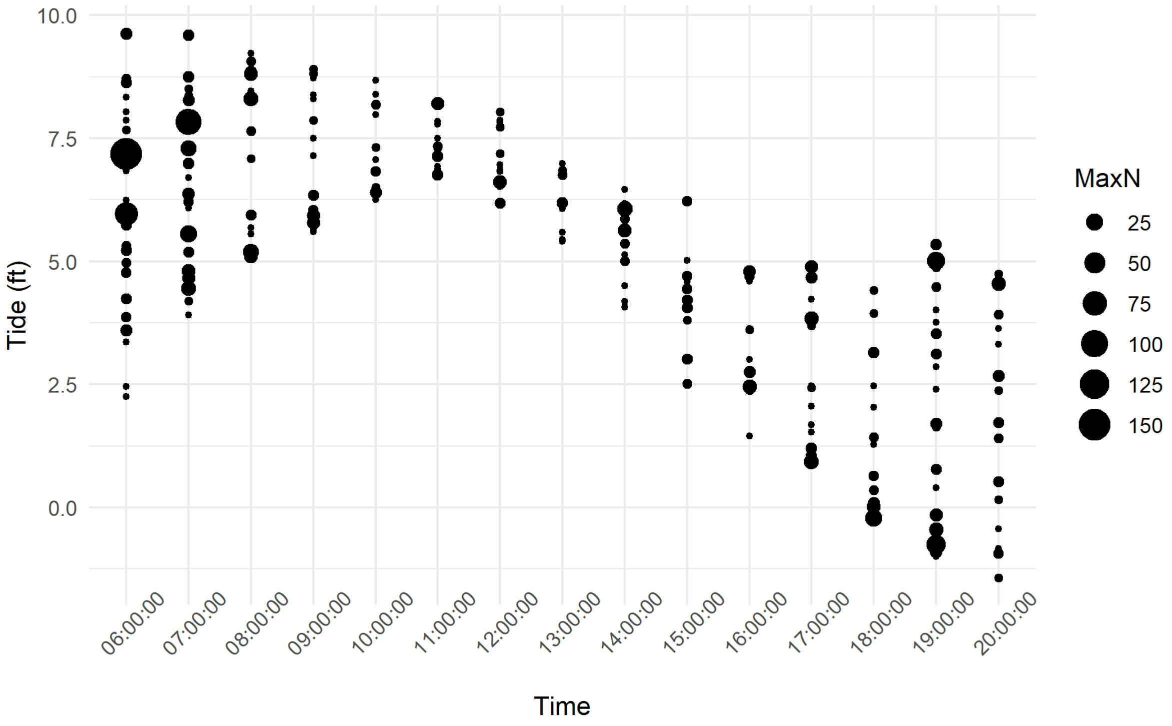

Figure 20: Tidal height in feet plotted against time of day (6:00-20:00) with dots representing the abundance (MaxN) of predators. Larger dots represent higher abundances of predators.

Fish movements can vary considerably depending on water temperature, with both high and low temperature thresholds limiting fish activity (Crawshaw 1984, Johansen et al. 2014). To understand how this could impact fish assemblages at the spawning site, I looked at how observed abundances varied with local water temperature. Temperature at the spawning site increased about 2.5°C from early May to early June and temperature variability doubled from 2.5°C in early May (temperature range of 10-12.5°C) to approximately 5°C from mid-May to early June (temperature range of 10-15°C; Figure 21). When looking at predator abundance with temperature, I found that the predator community I quantified was most abundant from approximately 10-14°C (Figure 22). I plotted abundance with temperature, date, and year and found that regardless of the year and date, the highest predator abundances were found in a temperature range of 10-14°C, a temperature range that was found throughout the sampling period (Figure 23). When temperatures were above 14°C, abundances were low, indicating that shallow water predator assemblage activity may be limited to some extent by temperature.

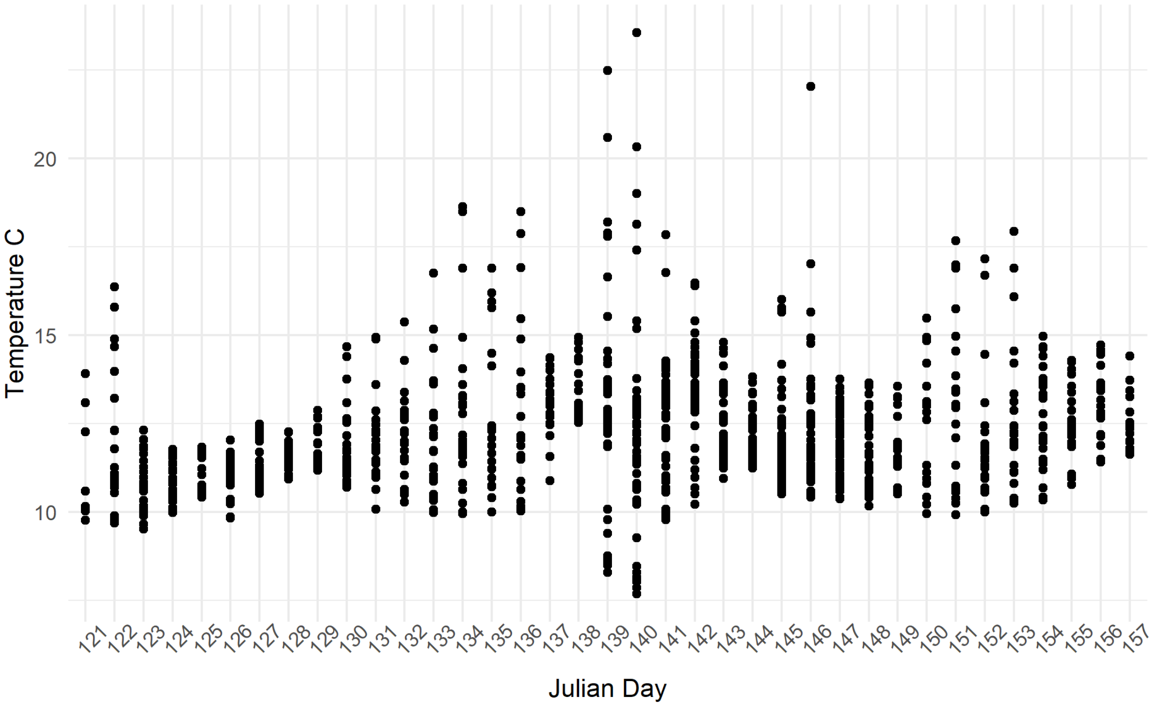

Figure 21: Scatter plot of temperature (°C) at the Cherry Point spawning site in 2021 and 2022 plotted against Julian day.

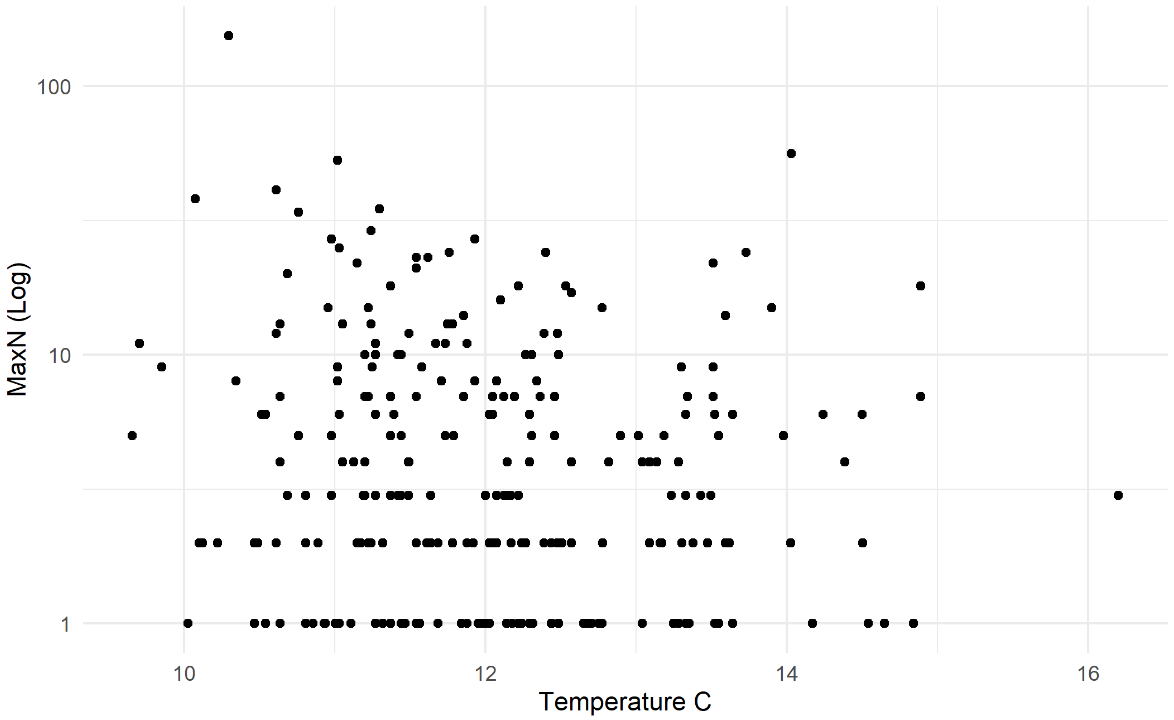

Figure 22: Scatter plot of predator abundance (MaxN) plotted against the temperature (°C) in which they were observed by the time-lapse camera. Abundance was set on a logarithmic scale to better assess patterns in the data.

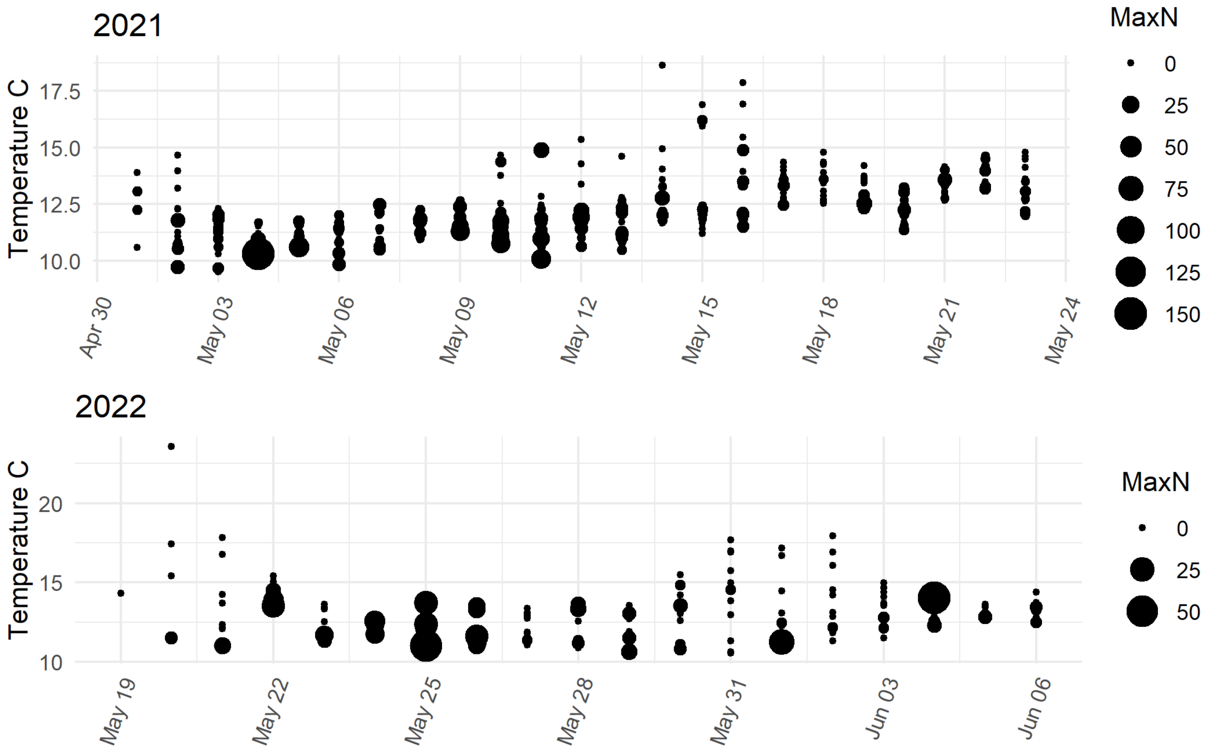

Figure 23: Scatter plots of temperature (°C) plotted against the sampling day (from time-lapse cameras). The size of the dot represents predator abundance (MaxN) with the largest dots depicting higher abundances. Scales differ between year panels.

Discussion

Mortality and Predation

Surf Scoters are thought to be a major predator of Pacific Herring eggs for the Cherry Point population. However, this study found that they were neither a major nor minor predator of the eggs during the study period. None of the three scoter species (surf, white wing, and black) were observed foraging at the Cherry Point spawning site for either sampling year, 2021 or 2022. The most prevalent avian predator was the Harlequin duck (*Histrionicus histrionicus*), which was observed foraging on the eggs during the first and second experiments. No avian predation was observed during the third experiment in late May and the last observations of birds in the area from the time-lapse cameras were on May 5th in 2021 and May 17th in 2022. The stop-over time for most scoter species in the Salish Sea is from mid-April to mid-May so they likely had left the area by the time of third experiment in late May 2022 (Lewis et al. 2007). For the first two experiments, Surf Scoters were present but in well-below-average abundances and it seems as though they did not make use of the spawn, either due to low egg biomass (potential inability to locate it), their own low abundance, abundance of alternative prey or a combination of these factors.

Due to the decline in spawning biomass, the Cherry Point population may have reached a density of eggs considered a “giving up density”, in which it is more energetically demanding for avian predators to look for spawn than to forage for other prey. The “giving up density” is defined as the density of resources within an area at which an individual abandons that area to forage elsewhere (Brown 1988, Hagy et al. 2017). If most avian predators are not able to locate the area where spawning occurred, this may give the Cherry Point population some reprieve from avian predation. If this is occurring at the Cherry Point spawning location, and the Cherry Point stock’s persistent low spawning abundance has been due to predation by scoters, we may start to see a rebound in the population of this stock due to the recent decrease in predation from avian predators. It is important to note that birds may have been deterred from foraging in the spawning area during the period of study due to the high amount of research activity in the area (i.e., boat surveys, experiment set up and sampling, and artificial spawning raft deployment and maintenance; part of the overall project but not described herein).

The exclusion experiment was not designed to exclude in-water predators smaller than 1-3/4" (size of mesh webbing) such as, snails, shrimp, crabs, fish, and amphipods. Throughout the experiment, snails and small crabs were observed climbing the stipes of *Sargassum muticum* presumably to forage on the eggs. Interestingly, high amphipod (Gammaridae and Caprellidae) abundances were observed at the spawning site while SCUBA diving and snorkeling during egg collection surveys. These relatively small predators may be having a larger effect on egg mortality than bigger predators. Previous studies on amphipod predation on fish eggs showed that significant amounts of egg loss can occur depending on amphipod size, abundance, and egg deposition (Deblois and Leggett 1993, Taylor and Dunn 2017). This indicates that small predators could be contributing to significant egg loss at localized scales; whether mortality from invertebrate sources is different in this stock than in other Salish Sea spawning stocks requires further investigation.

The predator exclusion experiment showed that predation by birds, large fish, and large invertebrates did not have a significant impact on egg mortality at the Cherry Point spawning site. While the time-lapse cameras showed large predators occupying and foraging at the spawning site, they did not seem to be causing high rates of egg mortality, as evidenced by the similarity in egg loss in the control and treatment plots. It is important to note, however, that even small amounts of predation may be having a relatively large impact on the population due to its small size and current limited spawning area.

The successful rebuilding of a significantly depleted population, like the Cherry Point stock, faces challenges beyond environmental conditions, including Allee effects. The Allee effect is defined as a positive relationship between the population abundance and the population growth rate, where small populations have low population growth (Hutchings 2014). The causes of low population growth include reduced probability of fertilization, predator saturation, reduced school size, and genetic drift (Myers et al. 1995, Hutchings 2014, The Salish Sea Pacific Herring Assessment and Management Strategy Team

2018). Studies have shown that when driven to very low abundances (density depensation), stock recovery is uncertain, and due to Allee effects and environmental conditions, recovery can take decades in some cases (Neubauer et al. 2013). While critical depensation was thought to be rare in marine fishes, two Atlantic Herring stocks have historically demonstrated possible depensation (Myers et al. 1995). With a decline in spawning biomass of 97%, the Cherry Point stock could be experiencing Allee effects that are inhibiting its recovery (The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018), and predation is further limiting population growth.

Shallow-water Assemblage and Habitat Use

We saw changes in community composition during and after the spawning events compared to before Pacific Herring arrived, suggesting that Cherry Point stock spawning events do influence the nearshore community. While the effect size was small, so was the area of deposited herring eggs; we might expect that the event's impact on the nearshore assemblage could be greater with larger population sizes. Historically, the Cherry Point herring stock was a much larger population, so it is likely that population decline has had implications for the numerous animals feeding on eggs and larvae, including the shallow-water, nearshore fish and invertebrate assemblage.

The habitat type of the spawning area is likely influencing what potential in-water predators are accessing the eggs. Fish prefer habitat that provides lots of physical structure within which to hide and forage and *Sargassum muticum* provides that structure more than other vegetation types in the Salish Sea, like eelgrass (Anderson 1984, Angel and Ojeda 2001, Diaz et al. 2003). Even with an abundance of *Zostera marina* and other suitable spawning substrate, the Cherry Point population appears to be choosing to spawn on *Sargassum muticum* (Shelton et al. 2014). The time-lapse cameras observed more abundance and diversity of species in the rocky intertidal zone with *Sargassum muticum* as the dominant alga present compared to nearby sandflats with *Zostera marina*. A herring population that is spawning in *Sargassum muticum* could be subjecting its eggs to higher predation due to its choice to spawn in high-complexity habitats with more fish abundance or diversity. In contrast to this hypothesis, it has been found that

Atlantic Herring (*Clupea harengus*) egg survival increases when spawning occurs in highly complex substrate (von Nordheim et al. 2018).

Other Sources of Mortality

Very high daytime temperatures were observed in 2021 and, due to the shallow spawning behavior of the Cherry Point stock, the eggs were exposed to temperatures as high as 26°C in early May. Exposure to air during low tide events can increase the pre-hatch mortality and developmental abnormalities of herring eggs (Jones 1972, Purcell et al. 1990). This exposure likely causes mortality due to hypoxemia, desiccation, and air-water thermal differential (Jones 1972, Villalobos et al. 2020, Russell et al. 2022). The shallow spawning behavior of the Cherry Point population could cause the eggs to be especially susceptible to these impacts.

Climate change will likely increase nearshore water temperatures, and this will have important implications for how the nearshore fish community accesses Pacific Herring eggs in the future (Xu et al. 2018, Khangaonkar et al. 2019, Murray and Klinger 2022). Previous studies on temperate fishes have shown species specific changes in foraging activity due to an increase in water temperature and these changes can result in localized changes in fish assemblages (Pörtner and Peck 2010, O'Connor and Booth 2021). During this study, the highest abundance of fish predators at the spawning site occurred in a relatively narrow range of 10-14°C and the predicted increase in water temperature of 1.5°C due to climate change could affect what fish are foraging in the spawning area and how successful they are (Khangaonkar et al. 2019). As for avian predators, scoter migration timing can be influenced by climate change (specifically changing snow cover duration) which in turn could affect their ability to forage at Pacific Herring spawning sites (Drever et al. 2012). The lipid-rich herring eggs are very important for some species, particularly birds, and so the effects of climate change could negatively impact the ability of some species to prey on this pulse resource (Odenweller 1975, Lewis et al. 2007, Cury et al. 2011).

Marine heatwaves are another consequence of climate change that have already impacted forage fish recruitment in the North Pacific (Arimitsu et al. 2021, Murray and Klinger 2022). Water temperature has significant effects on herring egg development and recruitment, with high temperatures accelerating development but also increasing mortality and developmental abnormalities (Alderdice and Velsen 1971, Stocker et al. 1985, Purcell et al. 1990). These studies have indicated that the optimal spawning temperatures for herring development are between 5-15°C with high rates of mortality and abnormalities occurring at 20°C and above (Alderdice and Velsen 1971, Takahashi et al. 1983), a temperature that the Cherry Point stock currently experiences, especially during day-time exposure during extremely low (-0.5m MLLW) tides. Increasing air and water temperatures, as well as marine heatwaves, will likely have a significant effect on the recruitment of the Cherry Point stock and is an area of research in need of greater study.

Not only does the shallow spawning leave eggs exposed during mid-day low tides, but their location in the swash zone makes them vulnerable to high wave energy. The effect of wave energy on egg loss is highly variable and localized but there is evidence that high wave energy events can drastically increase egg loss during the incubation phase (Rooper 1996). During this study, *Sargassum muticum* could show less resilience to high wave energy due to its holdfast than other vegetation types with different morphology, such as eelgrass which uses rhizomes. The Cherry Point stock's current spawning location at Birch Point is exposed to southerly winds and at times high wave energy. During the second experiment of this study, we saw massive egg mortality due to a high wind event that removed much of the *Sargassum muticum* that was used as spawning substrate. A 2014 study found no significant difference in egg loss by spawning substrate type (Shelton et al. 2014); however, localized impacts like wave action or predator abundance could mean certain vegetation types are less suitable for some populations, especially where beaches are subjected to high wave energy. It is important to note that although spawning substrate likely influences egg survival, other factors such as temperature, depth, spawning time and intensity, beach slope, silting, and wave action all combine to determine the success of recruitment (Haegele and Schweigert 1985, Shelton et al. 2014, von Nordheim et al. 2018).

The analysis of environmental variables also suggests that the composition of the shallow water community may be influenced by seasonal and temperature effects in addition to spawning; in general, abundances increased later in the spring. The Cherry Point stock may be especially influenced by these seasonal and temperature effects due to its spawning time in May when temperatures start to increase, the season transitions from winter to spring, and species diversity increases (Rice et al. 2012). The increase in fish abundances in spring that we observed in this study indicates that fish may be more active foragers during the Cherry Point spawning events than in other herring stocks' spawning events that occur earlier in the year.

Genetic drift, or loss of genetic diversity in small populations due to random chance, may have far reaching implications for the Cherry Point stock, in terms of its recovery, as well as the maintenance of overall genetic diversity of Pacific Herring in the southern Salish Sea (Petrou et al. 2021). It has been proposed that a decrease in population size changes the genetic structure of a stock, which reduces the individual fitness of these populations (Kramer et al. 2018). Pacific Herring in Alaska, British Columbia, and Washington have a population structure that is driven by reproductive timing which implies that variation in reproductive timing may be especially important in maintaining the genetic diversity of this species (Petrou et al. 2021). With its unique spawn timing and genetic diversity in the southern Salish Sea, conservation of the Cherry Point stock could aid in Pacific Herring's ability to adapt to a changing climate by maintaining genetic diversity.

As a migratory species, Pacific Herring occupy offshore areas much of the year, but little research has been done to identify where subpopulations are migrating. Because of this gap in understanding, we do not know where the Cherry Point population spends much of its life history. Washington State's Pacific Herring fishery is primarily a sport bait fishery that does not exceed 10% of the cumulative adult herring spawning biomass in South/Central Puget Sound, Hood Canal, and the Whidbey Basin; all other areas in the Puget Sound are closed to fishing, including the area around the Cherry Point spawning location (Sandell et al. 2019). In the Canadian waters of the Strait of Georgia, the Pacific Herring fishery is active with Roe Herring, Spawn-on-Kelp, and Food and Bait fisheries not to exceed 25% of unfished spawning biomass previous to 2021 and has since been reduced to 10% (Government of Canada 2017, Fisheries and Oceans Canada 2021). The Cherry Point population could be migrating into Canadian waters from summer until the spring spawning period and be subject to fishing in those areas. Until research is conducted on adult herring migrations by subpopulations, we will not know where these populations are migrating and what impacts individual populations are experiencing in these areas from fishing or other sources of mortality.

Conclusions

Use of time-lapse cameras to quantify fish abundance is an established but relatively new research method that comes with an array of benefits, drawbacks, and challenges (Peirano et al. 2016, Aguzzi et al. 2020). The benefits include the collection of abundance data for long, uninterrupted time periods that would otherwise be very labor intensive and costly if done with diver surveys or net surveys. The camera method also has a minimal impact on the local ecosystem and is non-lethal to fish. Unfortunately, the data collected is limited by camera field of view (area covered) and depth of field (how far away from the camera images are reliable) and dependent on fish movement in the vicinity of the camera. Cameras are unable to collect abundance data across a large spatial area, unlike net collections which can be conducted across larger areas. Wave and wind action also became an issue during this study, and due to turbid conditions, identification of fish proved challenging at times. Because of these factors, the cameras were not sufficient to provide an estimate of abundance in the classic sense, but do give us an idea of occurrence and index of local abundance that can be compared across timescales. This information would be very labor intensive if done with other methods. Time-lapse cameras proved useful in characterizing fish assemblages in shallow water habitats and future studies should utilize and improve upon this method, potentially using additional cameras for greater coverage.

This study demonstrated high mortality in herring eggs prior to hatching in the Cherry Point stock. However, egg mortality was similar in treatment and control sites, demonstrating little difference when large fish, avian, and invertebrate predators were excluded from foraging. Time-lapse cameras captured a diversity of potential predators and observations made during field work indicate an abundance of unmeasured but potentially important invertebrates associated with eggs at the site. Egg mortality at the Cherry Point spawning site is likely influenced by a multitude of factors including spawning time and habitat, water temperature, wind and wave activity, and numerous smaller fish and invertebrate species that take advantage of the lipid-rich food source.

As critical prey for many important species in the Salish Sea, understanding how predation impacts recruitment on Pacific Herring is important to understanding population dynamics. In a changing sea, climate change, habitat change, invasive species, and fishing may also affect the success of Pacific Herring and are important areas for future research. This study illustrates the complex nature of fish recruitment and the many variables that interact to ultimately determine the success of a population. While predation is an important driver in herring recruitment, there are complex ecological interactions influencing Pacific Herring recruitment that necessitate taking a more holistic approach.

References

Aguzzi, J., N. Iveša, M. Gelli, C. Costa, A. Gavrilovic, N. Cukrov, M. Cukrov, N. Cukrov, D. Omanovic, M. Štifanić, S. Marini, M. Piria, E. Azzurro, E. Fanelli, and R. Danovaro. 2020. Ecological video monitoring of Marine Protected Areas by underwater cabled surveillance cameras. Marine Policy 119:104052.

Alderdice, D. F., and F. P. J. Velsen. 1971. Some Effects of Salinity and Temperautre on Early Development of Pacific Herring (Clupea pallasi). Journal of the Fisheries Research Board of Canada 28:1545–1562.

Anderson, E., J. Lovvorn, D. Esler, W. Boyd, and K. Stick. 2009. Using predator distributions, diet, and condition to evaluate seasonal foraging sites: sea ducks and herring spawn. Marine Ecology Progress Series 386:287–302.

Anderson, M. J. 2017. Permutational Multivariate Analysis of Variance (PERMANOVA). Pages 1–15 Wiley StatsRef: Statistics Reference Online. John Wiley & Sons, Ltd.

Anderson, O. 1984. Optimal Foraging by Largemouth Bass in Structured Environments. Ecology 65:851–861.

Angel, A., and F. P. Ojeda. 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. Marine Ecology Progress Series 217:81–91.

Arimitsu, M. L., J. F. Piatt, S. Hatch, R. M. Suryan, S. Batten, M. A. Bishop, R. W. Campbell, H. Coletti, D. Cushing, K. Gorman, R. R. Hopcroft, K. J. Kuletz, C. Marsteller, C. McKinstry, D. McGowan, J. Moran, S. Pegau, A. Schaefer, S. Schoen, J. Straley, and V. R. von Biela. 2021. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. Global Change Biology 27:1859–1878.

Bishop, M. A., and S. P. Green. 2001. Predation on Pacific herring (Clupea pallasi) spawn by birds in Prince William Sound, Alaska. Fisheries Oceanography 10:149–158.

Brown, J. S. 1988. Patch use as an indicator of habitat preference, predation risk, and competition. Behavioral Ecology and Sociobiology 22:37–47.

Crawshaw, L. I. 1984. Low-temperature dormancy in fish. American Journal of Physiology-Regulatory, Integrative and Comparative Physiology 246:R479–R486.

Cury, P. M., I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Österblom, M. Paleczny, J. F. Piatt, J.-P. Roux, L. Shannon, and W. J. Sydeman. 2011. Global Seabird Response to Forage Fish Depletion—One-Third for the Birds. Science 334:1703–1706.

Deblois, E., and W. Leggett. 1993. Impact of amphipod predation on the benthic eggs of marine fish: an analysis of Calliopius laeviusculus bioenergetic demands and predation on the eggs of a beach spawning osmeriid (Mallotus villosus). Marine Ecology Progress Series 93:205–216.

Dexter, E., G. Rollwagen-Bollens, and S. M. Bollens. 2018. The trouble with stress: A flexible method for the evaluation of nonmetric multidimensional scaling. Limnology and Oceanography: Methods 16:434–443.

Diaz, R. J., G. R. Cutter, and K. W. Able. 2003. The importance of physical and biogenic structure to juvenile fishes on the shallow inner continental shelf. Estuaries 26:12–20.

Dionne, P., J. Evenson, M. M. Lance, S. F. Pearson, S. Tanedo, T. Sandell, K. L. Sobocinski, K. Spragens, and H. Stewart. 2022. Herring and Scoter Interactions Research Activity Final Report to Puget Sound Partnership. Page 44. Puget Sound Partnership.

Drever, M. C., R. G. Clark, C. Derksen, S. M. Slattery, P. Toose, and T. D. Nudds. 2012. Population vulnerability to climate change linked to timing of breeding in boreal ducks. Global Change Biology 18:480–492.

Dunlop, K. M., G. D. Ruxton, E. M. Scott, and D. M. Bailey. 2015. Absolute abundance estimates from shallow water baited underwater camera surveys; a stochastic modelling approach tested against field data. Journal of Experimental Marine Biology and Ecology 472:126–134.

Fisheries and Oceans Canada. 2021, December 16. Fisheries and Oceans Canada updates Pacific herring coast-wide harvest plan for 2021-22. News Release. https://www.canada.ca/en/fisheries-oceans/news/2021/12/fisheries-and-oceans-canada-updates-pacific-herring-coast-wide-harvest-plan-for-2021-22.html.

Fox, C., P. Paquet, and T. Reimchen. 2018. Pacific herring spawn events influence nearshore subtidal and intertidal species. Marine Ecology Progress Series 595:157–169.

Francis, T., D. Lowry, K. Biedenweg, E. Brown, J. Cleary, P. Dionne, T. Essington, C. Greene, L. Hauser, D. Hay, P. Hershberger, A. Kagley, T. Kulchyski, P. McCollum, C. Ormond, and T. Sandell. 2018. Assessment and Management of Pacific Herring in the Salish Sea: Conserving and Recovering a Culturally Significant and Ecologically Critical Component of the Food Web. Page 75.

Government of Canada, F. and O. C. 2017, June 19. Pacific herring 2021-2022 | Pacific Region | Fisheries and Oceans Canada. https://www.pac.dfo-mpo.gc.ca/fm-gp/mplans/herring-hareng-ifmp-pgip-sm-eng.html.

Haegele, C. W., R. D. Humphreys, and A. S. Hourston. 1981. Distribution of Eggs by Depth and Vegetation Type in Pacific Herring (Clupea harengus pallasi) Spawnings in Southern British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 38:381–386.

Haegele, C., and J. Schweigert. 1985. Distribution and Characteristics of Herring Spawning Grounds and Description of Spawning Behavior. Canadian Journal of Fisheries and Aquatic Sciences 42:s39–s55.

Haegele, C. W., and J. F. Schweigert. 1990. Egg Loss in Herring Spawns in Georgia Strait, British Columbia. Pages 309–322 Proceedings of the International Herring Symposium. Anchorage, Alaska.

Haegele, C. W. 1993. Epibenthic Invertebrate Predation of Pacific Herring, Clupea pallasi, Spawn in British Columbia. Canadian Field-Naturalist 107:83–91.

Hagy, H. M., J. D. Stafford, R. V. Smith, A. P. Yetter, C. S. Hine, M. M. Horath, and C. J. Whelan. 2017. Opportunity costs influence food selection and giving-up density of dabbling ducks. Journal of Avian Biology 48:804–814.

Hutchings, J. A. 2014. Renaissance of a caveat: Allee effects in marine fish. ICES Journal of Marine Science 71:2152–2157.

Johannessen, A. 1980. Predation on herring (Clupea harengus) eggs and young larvae. Page H:33, 12 p. ICES.

Johansen, J. L., V. Messmer, D. J. Coker, A. S. Hoey, and M. S. Pratchett. 2014. Increasing ocean temperatures reduce activity patterns of a large commercially important coral reef fish. Global Change Biology 20:1067–1074.

Jones, B. C. 1972. Effect of Intertidal Exposure on Survival and Embryonic Development of Pacific Herring Spawn. Journal of the Fisheries Research Board of Canada 29:1119–1124.

Kawakami, T., H. Okouchi, M. Aritaki, J. Aoyama, and K. Tsukamoto. 2011. Embryonic development and morphology of eggs and newly hatched larvae of Pacific herring Clupea pallasii. Fisheries Science 77:183–190.

Khangaonkar, T., A. Nugraha, W. Xu, and K. Balaguru. 2019. Salish Sea Response to Global Climate Change, Sea Level Rise, and Future Nutrient Loads. Journal of Geophysical Research: Oceans 124:3876–3904.

Kotterba, P., D. Moll, C. Hammer, M. A. Peck, D. Oesterwind, and P. Polte. 2017. Predation on Atlantic herring (Clupea harengus) eggs by the resident predator community in coastal transitional waters. Limnology and Oceanography 62:2616–2628.

Kramer, A. M., L. Berec, and J. M. Drake. 2018. Editorial: Allee effects in ecology and evolution. Journal of Animal Ecology 87:7–10.

Landis, W. G., and P. T. Bryant. 2010. Using Weight of Evidence Characterization and Modeling to Investigate the Cause of the Changes in Pacific Herring (Clupea pallasi) Population Dynamics in Puget Sound and at Cherry Point, Washington. Risk Analysis 30:183–202.

Lewis, T. L., D. Esler, and W. S. Boyd. 2007. Foraging Behaviors of Surf Scoters and White-Winged Scoters during Spawning of Pacific Herring. The Condor 109:216–222.

Lok, E. K., M. Kirk, D. Esler, and W. S. Boyd. 2008. Movements of Pre-migratory Surf and White-winged Scoters in Response to Pacific Herring Spawn. Waterbirds 31:385–393.

Lok, E. K., D. Esler, J. Y. Takekawa, S. W. D. L. Cruz, W. S. Boyd, D. R. Nysewander, J. R. Evenson, and D. H. Ward. 2012. Spatiotemporal associations between Pacific herring spawn and surf scoter spring migration: evaluating a ‘silver wave’ hypothesis. Marine Ecology Progress Series 457:139–150.

McGlinn, D., E. Szoecs, H. Wagner, F. G. Blanchet, J. Oksanen, M. Friendly, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, G. L. Simpson, P. Solymos, and M. H. H. Stevens. 2020. vegan: Community Ecology Package.

Murray, C. S., and T. Klinger. 2022. High PCO2 does not alter the thermal plasticity of developing Pacific herring embryos during a marine heatwave. Journal of Experimental Biology 225:jeb243501.

Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population Dynamics of Exploited Fish Stocks at Low Population Levels. Science 269:1106–1108.

Neubauer, P., O. P. Jensen, J. A. Hutchings, and J. K. Baum. 2013. Resilience and Recovery of Overexploited Marine Populations. Science 340:347–349.

von Nordheim, L., P. Kotterba, D. Moll, and P. Polte. 2018. Impact of Spawning Substrate Complexity on Egg Survival of Atlantic Herring (Clupea harengus, L.) in the Baltic Sea. Estuaries and Coasts 41:549–559.

O'Connor, C., and D. J. Booth. 2021. Response of estuarine fishes to elevated temperatures within temperate Australia: Implications of climate change on fish growth and foraging performance. Journal of Experimental Marine Biology and Ecology 544:151626.

Odenweller, D. 1975. Aspects of the Biology of the Shiner Perch in a Southern California Estuary. Transactions of the Western Section of the Wildlife Society 11:93–101.

Peirano, A., A. Bordone, S. Marini, P. Piazza, and S. Schiaparelli. 2016. A simple time-lapse apparatus for monitoring macrozoobenthos activity in Antarctica. Antarctic Science 28:473–474.

Petrou, E. L., A. P. Fuentes-Pardo, L. A. Rogers, M. Orobko, C. Tarpey, I. Jiménez-Hidalgo, M. L. Moss, D. Yang, T. J. Pitcher, T. Sandell, D. Lowry, D. E. Ruzzante, and L. Hauser. 2021. Functional genetic diversity in an exploited marine species and its relevance to fisheries management. Proceedings of the Royal Society B: Biological Sciences 288:20202398.

Pikitch, E., P. Boersma, I. L. Boyd, D. Conover, P. Cury, T. Essington, and S. Heppell. 2012. Little Fish, Big Impact: Managing a Crucial Link in Ocean Food Webs. Lenfest Ocean Program.

Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, P. D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, S. S. Heppell, E. D. Houde, M. Mangel, É. Plagányi, K. Sainsbury, R. S. Steneck, T. M. Geers, N. Gownaris, and S. B. Munch. 2014. The global contribution of forage fish to marine fisheries and ecosystems. Fish and Fisheries 15:43–64.

Pörtner, H. O., and M. A. Peck. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. Journal of Fish Biology 77:1745–1779.

Puget Sound Partnership. 2022, August 22. Forage Fish Vital Sign indicator. Lead Reporter PSEMP Forage Fish and Food Webs Work Group. Last updated: 8/22/2022. https://vitalsigns.pugetsoundinfo.wa.gov/VitalSign/Detail/33.

Purcell, J. E., D. Grosse, and J. J. Grover. 1990. Mass Abundances of Abnormal Pacific Herring Larvae at a Spawning Ground in British Columbia. Transactions of the American Fisheries Society 119:463–469.

Rajasilta, M., J. Eklund, J. Hänninen, M. Kurkilahti, J. Kääriä, P. Rannikko, and M. Soikkeli. 1993. Spawning of herring (Clupea harengus membras L.) in the Archipelago Sea. ICES Journal of Marine Science 50:233–246.

Rankine, P. W., and J. A. Morrison. 1989. Predation on Herring Larvae and Eggs by Sand-Eels Ammodytes Marinus (Rait) and HyperoplusLanceolatus (Lesauvage). Journal of the Marine Biological Association of the United Kingdom 69:493–498.

Rice, C. A., J. J. Duda, C. M. Greene, and J. R. Karr. 2012. Geographic Patterns of Fishes and Jellyfish in Puget Sound Surface Waters. Marine and Coastal Fisheries 4:117–128.

Rooper, C. N. 1996, August. Physical and biological factors affecting Pacific herring egg loss in Prince William Sound, Alaska. Thesis.

Rooper, C. N., and L. J. Haldorson. 1999. Consumption of Pacific herring (Clupea pallasi) eggs by greenling (Hexagrammidae) in Prince William Sound, Alaska. Fishery Bulletin 98:655–659.

RStudio Team. 2021. RStudio: Integrated Development Environment for R. RStudio, PBC, Boston, MA.

Russell, M., M. B. Olson, and B. A. Love. 2022. Surf smelt accelerate usage of endogenous energy reserves under climate change. PLOS ONE 17:e0270491.

Sandell, T., A. Lindquist, P. Dionne, and D. Lowry. 2019. 2016 Washington State Herring Stock Status Report. Page 87. Washington Department of Fish and Wildlife, WA.

Schweigert, J. F., and D. Fournier. 1982. A Model for Predicting Pacific Herring (Clupea harengus pallasi) Spawn Density from Diver Observations. Canadian Journal of Fisheries and Aquatic Sciences 39:1361–1365.

Schweigert, J. F., C. W. Haegele, and M. Stocker. 1985. Optimizing Sampling Design for Herring Spawn Surveys in the Strait of Georgia, B.C. Canadian Journal of Fisheries and Aquatic Sciences 42:1806–1814.

Schweigert, J. F., J. L. Boldt, L. Flostrand, and J. S. Cleary. 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. ICES Journal of Marine Science 67:1903–1913.

Shelton, A. O., and M. Mangel. 2011. Fluctuations of fish populations and the magnifying effects of fishing. Proceedings of the National Academy of Sciences 108:7075–7080.

Shelton, A., T. Francis, G. Williams, B. Feist, K. Stick, and P. Levin. 2014. Habitat limitation and spatial variation in Pacific herring egg survival. Marine Ecology Progress Series 514:231–245.

Siple, M. C., A. O. Shelton, T. B. Francis, D. Lowry, A. P. Lindquist, and T. E. Essington. 2018. Contributions of adult mortality to declines of Puget Sound Pacific herring. ICES Journal of Marine Science 75:319–329.

Stocker, M., V. Haist, and D. Fournier. 1985. Environmental Variation and Recruitment of Pacific Herring (Clupea harengus pallasi) in the Strait of Georgia. Canadian Journal of Fisheries and Aquatic Sciences 42:s174–s180.

Surma, S., E. Pakhomov, and T. Pitcher. 2018a. Energy-based ecosystem modelling illuminates the ecological role of Northeast Pacific herring. Marine Ecology Progress Series 588:147–161.

Surma, S., T. J. Pitcher, R. Kumar, D. Varkey, E. A. Pakhomov, and M. E. Lam. 2018b. Herring supports Northeast Pacific predators and fisheries: Insights from ecosystem modelling and management strategy evaluation. PLOS ONE 13:e0196307.

Surma, S., T. J. Pitcher, and E. A. Pakhomov. 2021. Trade-offs and uncertainties in Northeast Pacific herring fisheries: ecosystem modelling and management strategy evaluation. ICES Journal of Marine Science 78:2280–2297.

Takahashi, Y., J. Hirokawa, and A. Kumagai. 1983. Studies on the methods of egg-taking and incubation of Pacific herring, Clupea pallasi. Aquaculture Science 31:167–172.

Taylor, N. G., and A. M. Dunn. 2017. Size matters: predation of fish eggs and larvae by native and invasive amphipods. Biological Invasions 19:89–107.

Thomas, A. C., M. M. Lance, S. J. Jeffries, B. G. Miner, and A. Acevedo-Gutiérrez. 2011. Harbor seal foraging response to a seasonal resource pulse, spawning Pacific herring. Marine Ecology Progress Series 441:225–239.

Toresen, R. 1991. Predation on the eggs of Norwegian spring-spawning herring (Clupea harengus L.) on a spawning ground on the west coast of Norway. ICES Journal of Marine Science 48:15–21.

Villalobos, C., B. A. Love, and M. B. Olson. 2020. Ocean Acidification and Ocean Warming Effects on Pacific Herring (Clupea pallasi) Early Life Stages. Frontiers in Marine Science 7.

Willson, M. F., S. M. Gende, and B. H. Marston. 1998. Fishes and the Forest: Expanding perspectives on fish-wildlife interactions. BioScience 48:455–462.

Willson, M. F., and J. N. Womble. 2006. Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring. Reviews in Fish Biology and Fisheries 16:183–200.

Xu, W., T. Khangaonkar, K. Balaguru, B. Cope, and J. Arnold. 2018. Response of Salish Sea circulation and water quality to climate change and sea level rise. Salish Sea Ecosystem Conference.

Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse–consumer interactions. Ecological Monographs 80:125–151.

Zuur, A. F., E. N. Ieno, N. J. Walker, A. A. Saveliev, and G. M. Smith. 2009. GLM and GAM for Count Data. Pages 209–243 *in* A. F. Zuur, E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith, editors. Mixed effects models and extensions in ecology with R. Springer, New York, NY.