Resubmission

no

Descriptors

Category

Fishes and Invertebrates

Issue

- Fish disease ecology

Species

Atheresthes stomias, Clupea pallasii, Gadus macrocephalus, Hippoglossoides elassodon, Mallotus villosus, Oncorhynchus kisutch, Oncorhynchus nerka, Pleurogrammus monopterygius, Thaleichthys pacificus, Theragra chalcogramma

Large Marine Ecosystem(s)

Gulf of Alaska

Research Approach

Retrospective Studies

Keywords

climate change, disease, fisheries profitability, fisheries sustainability, global warming, parasite

Background

Context

In the summer of 2013, shorelines from Alaska to Mexico were littered with dying sea stars. Their bodies developed lesions that spread, causing arms to rot and fall off, internal organs to spill out, and the remainder of tissue to deflate and decay away. Later, the cause of this unprecedented wildlife die-off would be revealed: infection by a densovirus in the family Parvoviridae (Hewson et al., 2014). On some stretches of shoreline, 100% of sea stars were killed by this virus, a loss that is expected to have profound impacts on affected marine ecosystems.

The massive sea-star die-off of 2013 may have been driven by climate change (Hewson et al., 2014). Warming waters can create conditions that are conducive to parasite reproduction or compromise host immune defenses (Harvell et al., 1999; Harvell et al., 2002). Indeed, recent decades have brought many other explosions of infectious disease among marine organisms, including die-offs of endangered black abalone in California's Channel Islands (Lafferty and Kuris, 1993), sea urchins in the Caribbean (Lessios, 1988), and pilchards in

Australia (Whittington et al., 1997). These events appear to be increasing in frequency and magnitude, which begs the question: is climate change exacerbating the transmission of marine parasites?

Parasites represent a significant threat to the sustainability and profitability of wild fisheries (Lafferty et al., 2015); it is therefore vital that we understand whether climate change will intensify parasite transmission. Here, we outline our plan to assess how parasitism in the Gulf of Alaska responds to climate change and project how it will change into the future. Our goal is to provide actionable information that will allow commercial and subsistence stakeholders to anticipate and avoid future parasitic threats.

Lafferty et al. (2015) documented 67 instances in which parasites reduced the growth, survivorship, or marketability of commercially important marine fish species. Among these examples are anisakid nematodes, which cause filets to appear “wormy” and therefore render them unsalable (Bao et al., 2017a; Bao et al., 2017b; **Figure 1a**); copepod gill parasites, which can reduce growth and induce mortality, particularly in juvenile fish (Costello, 2006; **Figure 1b**); trematode flatworms, which can induce mortality (Jacobson et al., 2008) and reduce marketability (Buchmann, 1986) of fish (**Figure 1c**); monogenean flatworms, which reduce fish survival (Shirakashi et al., 2008; **Figure 1d**); and tapeworms, which reduce fish growth (Saksvik et al., 2001; **Figure 1e**). All of these groups of parasites exist in the Gulf of Alaska (Moles, 2007). As consumers, parasites redirect energy that might otherwise flow to predators or fisheries, “stealing” fish biomass from commercial and subsistence stakeholders.

These parasitic threats may be on the rise as oceans warm (Harvell et al., 1999; Marcogliese, 2001; Harvell et al., 2002; Harvell et al., 2004). Climate change may influence parasite transmission by (1) increasing rates of parasite reproduction or the length of the reproductive season for parasite species (Marcogliese, 2001), (2) shifting the ranges of hosts and parasites such that hosts are exposed to new parasite species, or (3) eroding host immune defenses that would otherwise keep parasites at bay (Chubb, 1980; Esch and Hazen, 1980). For example, industrially produced thermal effluent can increase the transmission to fish hosts of eye-infecting trematodes (Aho et al., 1982), intestinal tapeworms (Granath and Esch, 1983), and gill-infecting monogeneans (Pojmanska et al., 1980) by prolonging the parasites’ reproductive season (Aho et al., 1982). In the mid-1980s, the deadly oyster parasite dermo (*Perkinsus marinus*) expanded the northern boundary of its range from Long Island to Maine, killing oysters along the way (Ford, 1996; Cook et al., 1998). Elevated temperatures can reduce white blood cell and lymphocyte counts in fish, resulting in greater susceptibility to new infections (Esch and Hazen, 1980) and lower ability to tolerate existing infections (Chubb, 1980). A “rising tide” of disease may therefore be in store for warming oceans.

Alaska is experiencing much more rapid climate warming than the rest of the US (NOAA, 2013), and fishing is one of its most vital industries, bringing the state over $1 billion annually (NMFS, 2011). There is high potential for climate-driven impacts of parasitism on Alaskan fisheries, yet little research to suggest how parasitic threats might change with a changing Alaskan climate. Our proposed project aims to fill this gap.

Concept

Whether and why wildlife disease is on the rise are questions of profound importance for ecology, conservation, industry, and human society, but they are also notoriously troublesome questions to address. To understand temporal patterns in disease prevalence requires that we contrast contemporary conditions against appropriate “baseline” data, which can be difficult to come by. Some attempts to assess change in marine disease over time have made use of meta-analysis (Ward and Lafferty, 2004), but this approach can reach back only a few decades, to the publication dates of the earliest papers systematically catalogued in research databases. By the middle of the 20th century, ocean ecosystems had already been radically altered by climate change (Lotze et al., 2006). If marine disease is on the rise, we will need more than a few decades of data to detect it.

To date, our field's ability to "hindcast" disease change has been hobbled by an absence of historical data on marine disease. **A grant from the North Pacific Research Board will enable our team to "turn back the clock", generating primary data on the dynamics of marine disease over long time profiles** and at unprecedented temporal, spatial, and taxonomic resolutions. In an effort of ambitious scope, we will extract information on the historical abundance of marine parasites from the University of Washington Fish Collection, the University of Alaska Museum of the North, and other natural history museums across the country. The proposed project will provide the world's first glimpse of disease dynamics in a "pristine" ocean, and will indicate whether contemporary oceans are experiencing a rising tide of disease.

Objectives

1. Assess long-term (1880s–present day) trends in the abundance of parasites among 10 Gulf of Alaska fish species by performing parasitological dissection of liquid-preserved museum specimens held in the UW Burke Museum, UA Museum of the North, and other natural history collections.
2. Use the resulting database of historical parasite abundance to identify the Gulf of Alaska regions experiencing the greatest and the least change over time in parasite abundance.
3. Assess the degree to which parasite abundance may be driven by climate warming for each parasite taxon detected, by regressing annual sea surface temperature against parasite abundance, using publicly available climate datasets.

Design and Approach

Design

In the basements of thousands of museums around the world, biological collections languish. An underutilized resource, museum specimens are a repository of information on historical parasite assemblages, and perhaps our only means of reconstructing these assemblages. Many disease agents (i.e., parasites that cause disease in marine fish) are preserved alongside their vertebrate and invertebrate hosts, whether stored in ethanol or formalin. Our preliminary dissections at the California Academy of Sciences (San Francisco, CA), the Smithsonian Institution's National Museum of Natural History (Washington, DC), and the UW Fish Collection (Seattle, WA) have confirmed that delicate parasites are preserved and detectable, even in decades-old specimens (**Figure 2**). We will use these resources to develop time profiles of parasite abundance and diversity, encompassing more than 130 years and bracketing major turning points in the history of ocean ecosystem degradation. This approach will be a first step toward developing an unbiased, empirical estimate of historical rates of marine parasitism – data that can be used to test whether the perceived rise of disease is real or an artifact of improved observation and reporting.

The Gulf of Alaska is an economic engine for the state, but this ecosystem may be under threat from a "rising tide" of marine disease. Our preliminary work has already demonstrated an alarming trend of increasing infection in a nearby ecosystem – a trend that could threaten the future viability of Gulf of Alaska fisheries. *Clavinema mariae* is a nematode parasite of benthic fishes that is common in English sole (*Parophrys vetulus*) of Puget Sound, WA. As a large, easily visible parasite that renders fish unmarketable, *C. mariae* was responsible for the mid-20th century closure of the English sole fishery in a large swath of Puget Sound (Holland, 1954; Holland, 1969). We obtained historical records of its abundance from the literature and from unpublished Washington Department of Fish and Wildlife data, and resampled the same locations using the same methods in 2017, to compare historical and contemporary *C. mariae* abundance (**Figure 3a**; Howard et al., in review). We also obtained museum specimens of English sole, collected between 1930 and 2016, and examined them for *C. mariae* burden (**Figure 3b**; Howard et al., in review). Both the historical data and museum specimen approaches demonstrated increases over time in *C. mariae* abundance, with robust agreement between the two approaches. In addition to documenting a **previously unrecognized eightfold increase in the burden of an economically important parasite**, this work demonstrates that parasitological examination of liquid-preserved museum specimens can produce reliable data on long-term trends in parasite abundance, at a much greater temporal resolution (**Figure 3b**) than is possible to obtain from historical records (Howard et al., in review).

In the project proposed here, we will characterize long-term change in the burden of parasitic disease among economically important marine fishes of the Gulf of Alaska and assess whether this long-term change might be driven by global warming. We hypothesize that – like *Clavinema mariae* in English sole of Puget Sound – several of these parasites have increased substantially in abundance over the past decades. We also hypothesize that the abundance of some of these parasites will be positively correlated with sea surface temperatures, and driven by global warming. The information we propose to gather will identify those parasites that are on an upward trajectory, and therefore likely to pose a threat to Gulf of Alaska fisheries in a warming world.

Approach

In the next two years, our team will quantify change in Gulf of Alaska parasite assemblages by assessing the parasite burden of fish museum specimens collected at different points in time. We will choose 10 representative host species (**Table 1**) across the Gulf of Alaska food web, source museum lots of these species from the UW Fish Collection, the UA Museum of the North, and other nationally recognized natural history collections, perform parasitological dissections of these museum specimens, and use the resulting data to reconstruct trajectories of change for the entire parasite fauna of each species. That is, we will build a timeline, as in **Figure 3b,** for each of the parasite taxa infecting these 10 hosts. Aggregating across parasite taxa, our team will (Objective 1) assess whether there has been a general trend of increasing or decreasing infection over time, (Objective 2) identify the regions of the Gulf of Alaska that have experienced the most change in infection, and (Objective 3) isolate the potential role of climate warming in these changing infection patterns.

Hypotheses and predictions. We posit the following hypotheses and predictions for each of our three objectives:

H1. Climate change is driving persistent increases in sea surface temperature throughout coastal Alaska, and several lines of evidence suggest that this might exacerbate parasite transmission, resulting in rising parasite burdens in a warming ocean.
P1. Although we expect variability among parasite species, we anticipate a general trend of increasing parasite abundance through time, from 1880 to the present day.

H2. Parasites are often distributed heterogeneously, with “hot spots” concentrating in areas of high transmission. Higher latitude areas are experiencing the most rapid climate change, so we would expect parasite “hot spots” to be more common in high-latitude regions than in low-latitude regions.
P2. We expect substantial heterogeneity in parasite abundance among regions, with parasite “hot spots” concentrating at high latitudes within the Gulf of Alaska and parasite “cold spots” concentrating at low latitudes.

H3. Increasing temperature can increase parasite reproductive rates, lengthen parasite reproductive seasons, and erode host immunity. We therefore expect to find that parasites are positively associated with climate change-driven increases in temperature.
P3. Although we expect variability among parasite species, we anticipate positive correlations between parasite abundance and temperature when averaging across Gulf of Alaska parasite species.

Study design. We will dissect individuals of each fish species from at least five points in time, spanning at least an 80-year range (**Table 1**). We will target 30 individuals from each time point for all species. The selected species span nearly the entire range of trophic levels for fishes in the Gulf of Alaska (see column "TL" in **Table 1**). This diversity of fish host species will allow us to draw conclusions about parasitic infection across the Gulf of Alaska food web, and will facilitate future research regarding the role of host ecology in parasite change over time.

Power analysis. We are interested in detecting change over time in the abundance of parasites in marine fishes. To ensure that our study has sufficient replication to detect such a change, we performed a power analysis. Some of the assumptions for our power analysis were drawn from a previous study of the abundance of the nematode *Clavinema mariae* in English sole (*Parophrys vetulus*) of Puget Sound (Howard et al., in review; **Figure 3**). We created a simulated dataset of random Poisson variables for parasite abundance, which mirrored the properties of the *C. mariae* dataset (i.e., from the *C. mariae* dataset, we calculated the magnitude of change in parasite abundance over time and mean and variance of parasite abundance at each time point) and which was 80 years long (i.e., the shortest time series proposed in **Table 1**). We generated 999 iterations of this dataset at our proposed level of replication (150 replicates) and found the proportion of simulated datasets within each replication group that detected a significant ($p < 0.05$) change over time. We found that power = 82% for the proposed experimental design (150 replicates). A statistical rule-of-thumb is that studies should have at least an 80% probability of detecting an effect where an effect exists (Cohen 1988), so we conclude that our proposed level of replication is sufficient to detect realistic degrees of change over time in parasite abundance for each of the ten host species.

Timeline. We propose to dissect 1,500 fish in total (**Table 1**). In the past, a single dissector (CLW) working alone has completed ~2,000 fish dissections in 2 years of work. With the personnel proposed (1 Masters student, with assistance from at least 3 undergraduate capstone students), we believe that we can complete all specimen acquisition and dissection in the first 1.3 years of the project, to be followed by data cleaning, curation, analysis, and manuscript preparation, as well as presentation of results at the Alaska Marine Science Symposium (see Timeline and Milestones document).

Personnel. Dissections will be carried out by the Masters student who would be funded by this grant, but this student will have significant assistance from undergraduate researchers. We will train at least three undergraduate capstone students as dissection assistants, and these trained assistants will both facilitate the completion of the 1,500 proposed dissections and obtain data for their own capstone projects. Each student's capstone project will focus on questions that are complementary to the larger goals of the project. For example, capstone projects might address the following questions: (1) Does the rate of change over time in parasite abundance vary depending upon the trophic level of the host species? (2) Does the rate of change over time in parasite abundance vary depending upon the density of the host species (as reflected in fisheries assessments)? (3) Does the rate of change over time in parasite abundance vary depending upon the latitude of collection of the host (indicating differential effects of climate change across latitudes)? These students will gain a valuable experience conducting their own, independent, cutting-edge parasite ecology research, while simultaneously advancing the larger goals of the project.

Specimen acquisition. The UW Fish collection has served the archival center for NOAA's Alaska Fishery Science Center for more than two decades, and is home to the largest collection of Alaskan fishes in the world. We have already received approval for the proposed use of specimens outlined in Table 1 from co-PI Luke Tornabene (Curator of Fishes, UW Fish Collection) and Unfunded Collaborator J Andrés Lopéz (Curator of Ichthyology and Aquatics, University of Alaska Museum of the North). The majority of specimens we propose to semi-destructively sample will originate from the UW Fish Collection and UA Museum of the North, but for the remainder of specimens, we have reached similar agreements with the managers of other collections (e.g., California Academy of Sciences, Smithsonian Institution's National Museum of Natural History). We will use the collections of museums other than UW and UA primarily to obtain specimens from earlier time points (**Table 1**, final column).

Specimen meta-data acquisition. The fish to be targeted for this study are extensively documented in the databases of their respective museums and on FishNet2, a collaborative geo-referencing project that aggregates meta-data for specimens in ichthyology collections at natural history museums across North America (FishNet2 Portal, 2017). Currently, an impressive 93% of all specimens from the UW Fish Collection have been geo-referenced on FishNet2. We will collect meta-data for each fish from two sources: (1) data recorded on paper tags included with the specimen and (2) data associated with the specimen in FishNet2. Metadata fields will include institutional catalog number, host Latin name, preparation type, latitude and longitude of collection, collection locality (i.e., the name of the collection site), collection date, depth, and collector/collection expedition ID. For most of these specimens, precise latitudes and longitudes of collection will be available, either on the paper tag, in the database, or both. Where geographic coordinates are not available, we will either: (1) use logbooks from the collection expedition (typically archived at the museum where specimens are held) to find the latitude and longitude of collection or (2) use the collection locality information to estimate an approximate latitude and longitude of collection in Google Earth. If neither of these methods yield geographic coordinates, the specimen will not be evaluated, and will be substituted with a specimen for which precise latitude and longitude values can be obtained. Space is a key component of the analyses proposed below, and we will ensure that each fish included in the analysis is associated with a reliably estimated spatial coordinate.

Specimen dissection protocol. For each individual fish selected for analysis, our team will perform a limited parasitological dissection that minimizes damage to specimens. All specimens will be photographed, measured (total length, fork length, and standard length), and weighed prior to dissection. We will then make a longitudinal incision along the ventral surface of the fish, from the vent through the pectoral girdle to the isthmus. We will remove the organs of the body cavity (stomach, cecae, intestine, gall bladder, spleen, liver, gonads) into individual dishes. The gill arches and heart will also be removed through this incision. Each organ will be examined separately under a dissecting microscope for parasites. Any parasites found in this material will be identified, counted, and vouchered. Finally, the incision will be spread open widely and placed over a strong light source, to indicate the presence of any nematode or cestode larvae in the muscle tissue. Organs will be returned to the body cavity and incisions will be stitched closed after the dissection is complete, preserving the external morphology of the fish specimen.

Parasite identification and cataloging. Once parasites are removed from fish, they will be studied under magnification and identified to the lowest possible taxonomic level using parasitological references (e.g., Schultz, 1969; Skryabin, 1991; Khalil et al., 1994; Gibson et al., 2002; Kabata, 2003; Bray et al., 2005; Bray et al., 2008), host-specific literature resources, and, for difficult identifications, with assistance from parasitologists with appropriate taxonomic expertise. We will then prepare parasites for cataloging in their collection of origin or at the National Parasite Collection at the Smithsonian Institution, at the discretion of the curator.

Acquiring climate data. We will obtain publicly available, reconstructed climate data for the Gulf of Alaska, matched to the temporal scope of our parasitological data. The primary climate dataset we have selected provides reconstructed sea surface temperatures for central, southeast, and southwest Gulf of Alaska and the Haida Gwaii/Queen Charlotte Islands at annual intervals from 1950–1997 (**Figure 4**; Bograd et al., 2005). We will assign each individual fish's collection location to the nearest of these four geographic regions and investigate the data both spatially (how do regional differences in temperature drive regional differences in parasite abundance?) and temporally (how does changing temperature through time drive changes in parasite abundance?).

The dataset described above provides high spatial resolution, but has a relatively narrow temporal range (47 years, 1950–1997); some of the fish samples to be targeted will have been collected before or after this time period. We will therefore perform another analysis using an alternative dataset that fills in temporal gaps by providing annually resolved sea surface temperatures averaged across the Gulf of Alaska from 1750–1983 (D'Arrigo et al., 1999). This dataset provides a broad temporal range (103 years, from 1880, the first year in which we have fish samples, to 1983, the end of the temperature dataset), but lacks the spatial resolution of the primary climate dataset. We will use both datasets to capitalize on the advantages and compensate for the disadvantages of each.

Both of these datasets reflect inter-annual and longer-term variability in oceanic climate, including El Nino Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO; Wiles et al., 1996; Wiles et al., 1998; Wilson et al., 2007; Wiles et al., 2014). We are especially interested in shifts in parasite assemblages that might have accompanied the substantial PDO shift of 1976 (NOAA, 2013; see gray vertical bar in **Figure 4**)

Statistical analysis

Objective 1. We will assess long-term trends in parasite abundance for each host–parasite combination by modeling parasite abundance (# parasites / host) in a fixed-effects, generalized linear model with year as a fixed factor and negative binomial error, using the glmmADMB package in R. To test for spatial autocorrelation, we will use Moran's I, implemented using the *Moran.I()* function of the fields library in R. We will also produce a spatial variogram, implemented in the gstat library in R, to test for a relationship between distance and semivariance, which would indicate spatial autocorrelation in the dataset. In the absence of spatial autocorrelation, we will proceed with analysis. If spatial autocorrelation is indicated, we will instead use hierarchical regression models for the Objective 1 analysis step.

From the regressions performed for each host–parasite combination (described in the preceding paragraph), we will extract the estimate and standard error of the slope of the relationship between parasite abundance and time. We will then analyze whether the mean trajectory of change over time in parasite abundance (aggregated across parasite species) is positive (indicating increasing parasitism over time), negative (indicating decreasing parasitism over time), or neutral (indicating no change over time), by using slopes as effect size estimates into a meta-analytic, fixed-effects general linear model in the R package metafor (after Wood et al. 2014). From this analysis, we will be able to conclude whether parasite abundance in the 10 focal host species has generally increased, decreased, or remained the same over the study period (1880–2016).

Objective 2. Are there host species or regions of the Gulf of Alaska that are experiencing significant change in parasite assemblages? We will identify hotspots of parasite abundance using spatio-temporal cluster analysis. We will perform space–time scanning with SaTScan v9.4.4 to find clusters of parasitic infection across host and parasite species.

There are unique challenges to overcome in finding space–time clusters of parasite abundance. Our samples originate from natural history collections, and therefore represent sampling points that are disjunct and distant in space. In order to account for the stretches of space across which no sampling occurred, we will use discrete scan statistic models, where the geographical locations for each datum (i.e., museum specimen) are non-random and fixed by the user (Kulldorff, 2015). Spatial randomness in the distribution of parasite abundance is then evaluated with respect to these selected observation points, rather than testing the null hypothesis that each observation has a random spatial location (Kulldorff, 2015). The use of discrete scan statistics therefore allows us to account for the fact that the sampling locations of the 1,500 fish we will target are non-random.

To find space–time clusters of parasite abundance, we will use discrete Poisson cluster analysis, which assesses whether there is significant clustering of parasites compared to the underlying distribution of sampled fish. We will use a multivariate approach to simultaneously scan across the entire dataset (all parasites, all hosts) for joint and separate clusters of each parasite species and each host. With a multivariate approach, we will combine the power of multiple datasets (where the number of datasets = number of parasite species detected across all hosts) to detect joint clusters and test whether parasites of different species and different hosts are correlated or uncorrelated in space and time. SaTScan's search for clusters will be performed using circular, spatial, moving, varying diameter windows. The SaTScan algorithm detects a cluster in space and time when there are more cases observed within the scanning window than expected; we will define clusters as spatial aggregations up to

10% of the detected parasites and temporal windows up to 40 years in duration. The statistical significance of detected clusters will be assessed using the log-likelihood ratio statistic and the corresponding p-value will be obtained using 999,999 Monte Carlo simulations (Kulldorff, 2015).

The output of this analysis will be a list of coordinates (in space and time and across host species) and radii for "hot spots" of high parasite abundance. From this analysis, we will be able to identify geographic regions of the Gulf of Alaska that have undergone substantial increases in parasite abundance over time. We will also be able to pinpoint the temporal onset of these changes (the temporal component of the hotspot) and the host species contributing most to the change.

This analysis will be repeated to find "cold spots" of low parasite abundance. The model form will be identical, but the algorithm will search for "anti-clusters" of parasitic infection instead of clusters of parasitic infection – areas where there are fewer cases observed within the scanning window than expected. The output of this analysis will be a list of coordinates (in space and time and across host species) and radii for "cold spots" of low parasite abundance.

Hot spots and cold spots of parasite abundance will be visualized in both static and dynamic maps using ArcGIS. The resulting output will allow us to identify the Gulf of Alaska regions experiencing the greatest and the least change over time in parasite abundance.

Objective 3. Are changes in parasite abundance associated with long-term climate trends? We will assess whether trends in parasite abundance are associated with climate for each host–parasite combination, by modeling parasite abundance (# parasites / host) in a mixed-effects, generalized linear model with temperature as a fixed factor, year as a random effect, and negative binomial error, using the glmmADMB package in R. We will perform this analysis twice, using two different datasets for the climate fixed effect: (1) sea surface temperature data available for only subset of the data (1950–1997) but with geographically specific temperature estimates for separate regions of the Gulf of Alaska (Bograd et al., 2005) and (2) sea surface temperature data available for a larger proportion of the data (1880–1983), but where temperature estimates are averaged over the entire Gulf of Alaska (D'Arrigo et al., 1999). Each of these climate datasets has benefits and drawbacks, but we expect to obtain similar results across the two; by using two independent metrics of climate, we will ensure that our findings are robust to variation in the source of climate data. The output of this analysis (climate coefficient) will indicate the degree to which parasite abundance may be driven by climate warming.

To test how both spatial and temporal variability in temperature influence parasite abundance, we will repeat the SaTScan analysis above (Objective 2), but will add climate (from Bograd et al., 2005) as a covariate. The climate dataset chosen for this part of the analysis (Bograd et al., 2005) makes separate estimates of historical sea surface temperature (1950–1997) for central, southeast, and southwest Gulf of Alaska and the area around the Haida Gwaii/Queen Charlotte Islands. Between 1950 and 1997, sea surface temperature in these four regions tended to vary together, with a few important departures among regions (Bograd et al., 2005); comparing these departures would be an informative test of how spatial variability in temperature might drive spatial variability in parasite load. For each fish dissected, we will assign the specimen to the Gulf of Alaska region (central, southeast, and southwest Gulf of Alaska and the area around the Haida Gwaii/Queen Charlotte Islands) nearest its collection locality; we will then use the dataset in Bograd et al. (2005) to extract a value for temperature for the year of fish collection in the geographic region of collection (i.e., central, southeast, or southwest Gulf of Alaska or the area around the Haida Gwaii/Queen Charlotte Islands). The output of this analysis will be a list of coordinates (in space and time and across host species) for "hot spots" of high parasite abundance and "cold spots" of low parasite abundance, and an estimate of how the covariate temperature contributes to these patterns. From this analysis, we will be able to identify the degree to which spatial and temporal variability in temperature drive hot and cold spots of parasite abundance.

Conclusion

Our project will reveal whether parasitism is increasing in the Gulf of Alaska (Objective 1), which regions are at greatest risk (Objective 2), and whether climate change is likely to exacerbate parasite burdens into the future (Objective 3). Work in other ecosystems suggests that climate change is likely to intensify parasite transmission, threatening fisheries sustainability and profitability. Our project is a vital first step toward understanding the threat posed by parasitism to the economically valuable fisheries of the Gulf of Alaska.

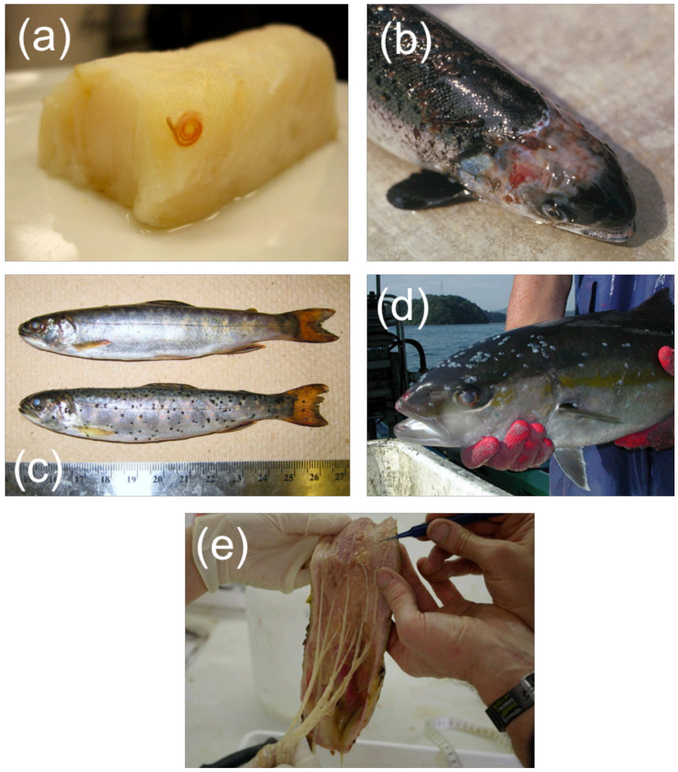

Figure 1. Parasites represent a significant threat to fisheries profitability and sustainability: (a) cod filet containing a single, coiled anisakid **nematode**, reproduced from (Ramanan et al., 2013); (b) Atlantic salmon with loss of skin over the head, due to heavy infestation by the **copepod** *Lepeophtheirus salmonis,* reproduced from (Costello, 2006); (c) uninfected brown trout (top) and brown trout infected with *Neascus* spp. **trematodes** (bottom), reproduced from (Wildlife, 2017); (d) **monogenean** flatworms (*Benedenia seriolae*) infecting the skin of a yellowtail kingfish, courtesy of Ingo Ernst, South Australia Museum; (e) **tapeworms** clinging to the intestinal lining of an ocean sunfish, courtesy of Richard Saunders, South Australia Museum.

Figure 2. (a) Specimens in the Ichthyology Collection at the California Academy of Sciences, San Francisco, CA. (b) Some metazoan parasites recovered from dissections of Atlantic cod (*Gadus morhua*) and spiny dogfish (*Squalus acanthias*) at the Smithsonian Institution's National Museum of Natural History in Washington, DC.

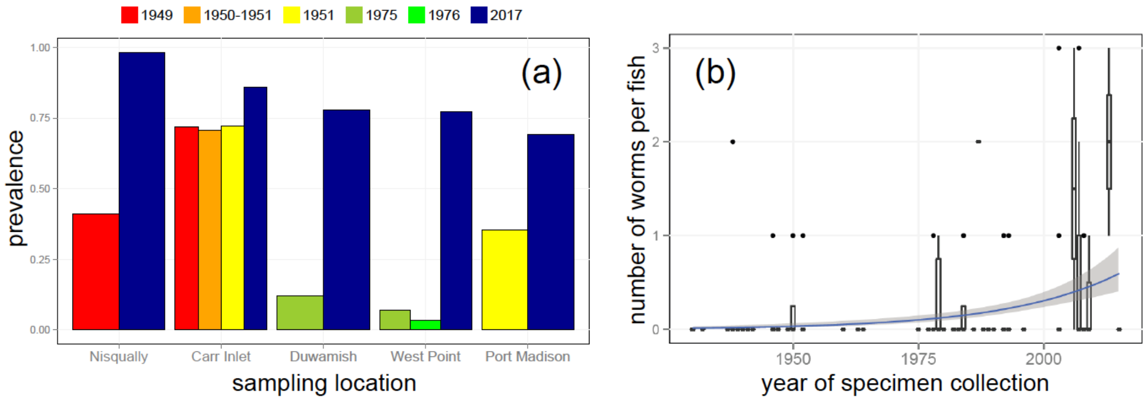

Figure 3. (a) Historical (1949–1976) and contemporary (2017) prevalence of *Clavinema mariae* in English sole at five sites, ordered from southernmost to northernmost. (b) Abundance of *Clavinema mariae* in specimens of English sole from the UW Fish Collection, as a function of year of the specimen's collection. From Howard et al. (in review).

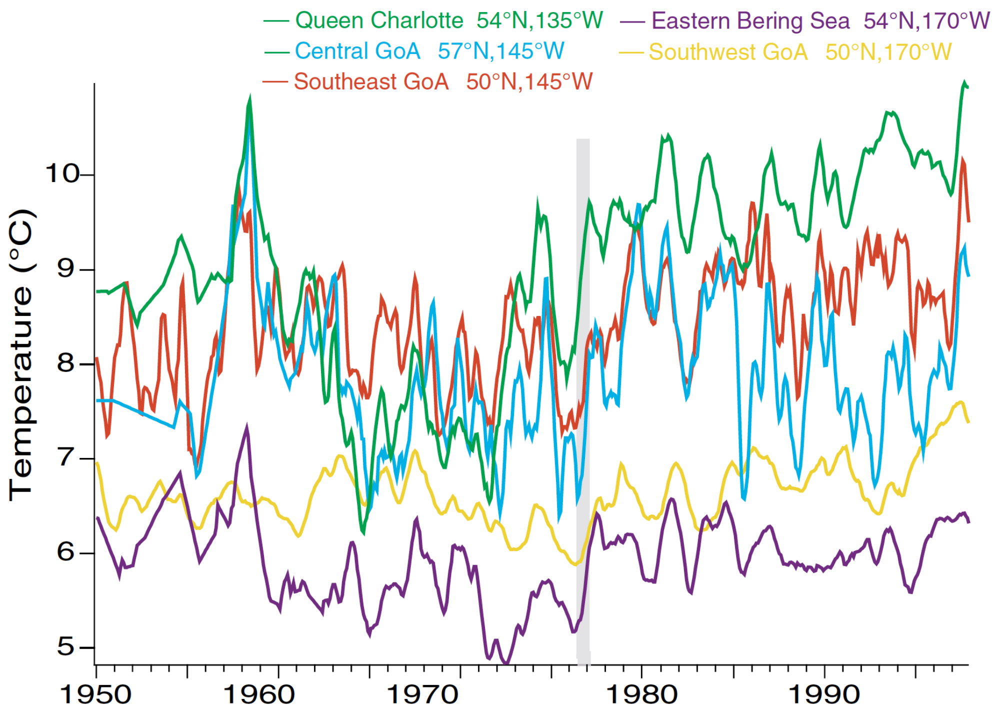

Figure 4. Reconstructed sea surface temperature values for five geographic regions in and around the Gulf of Alaska. Reproduced from Bograd et al. (2005).

Table 1. *Ten representative host species to be targeted for parasitological dissection. TL = trophic level (from FishBase.org), # targeted = the number of specimens we aim to dissect from each species, # available at UWFC = # specimens originally collected within Alaskan waters and held at the UW Fish Collection, # available at UAM = # specimens originally collected within Alaskan waters and held at the University of Alaska Museum of the North, # available across all museums = # specimens originally collected within Alaskan waters and held at all natural history museums in North America, including the UWFC. Years of collection of the oldest and most recent specimens are indicated in parentheses.*

Host common name	**Host Latin name**	**TL**	**# targeted**	**# available at UWFC (date range)**	**# available at UAM (date range)**	**# available across all museums (date range)**
Coho salmon	*Oncorhynchus kisutch*	4.2	150	437 (1923–2003)	675 (1955–2013)	4504 (1877–2013)
Pacific cod	*Gadus macrocephalus*	4.2	150	710 (1931–2013)	102 (1957–2014)	1218 (1880–2014)
Arrowtooth flounder	*Atheresthes stomias*	4.2	150	165 (1928–2013)	410 (1957–2007)	1323 (1880–2013)
Flathead sole	*Hippoglossoides elassodon*	3.7	150	1758 (1928–2013)	281 (1956–2013)	2819 (1928–2013)
Walleye pollock	*Theragra chalcogramma*	3.6	150	778 (1920–1989)	331 (1957–2015)	2368 (1880–2015)
Sockeye salmon	*Oncorhynchus nerka*	3.5	150	584 (1923–2009)	783 (1956–2013)	3897 (1877–2013)
Atka mackerel	*Pleurogrammus monopterygius*	3.4	150	311 (1930–2010)	21 (1962–2009)	446 (1930–2012)
Eulachon	*Thaleichthys pacificus*	3.3	150	204 (1934–2013)	190 (1957–2013)	618 (1879–2013)
Capelin	*Mallotus villosus*	3.2	150	1015 (1929–2013)	825 (1956–2015)	17,655 (1879–2015)
Pacific herring	*Clupea pallasii*	3.2	150	3379 (1923–2011)	1232 (1955–2016)	4986 (1880–2016)

Management or Ecosystem Implication

Those who do not learn from the past are doomed to repeat it. Here, we propose to learn about how climate has driven parasite burdens in the past, so that we may anticipate parasitic threats on the horizon. Given the significant negative impacts of parasites on fisheries profitability and sustainability (**Figure 1**; Lafferty et al., 2015), this research is vital to the future of the Gulf of Alaska's commercial and subsistence fisheries.

The awesome power of parasites has long been recognized in fisheries management (Lafferty et al., 2015). Take as an example the nematode *Clavinema mariae* in English sole (*Parophrys vetulus*) of Puget Sound. This parasite is large, deep red, and highly visible in sole filets, and renders sole unmarketable for human consumption. It became so abundant in south Puget Sound in the 1940s that the English sole fishery became unprofitable and was closed (Holland, 1954; Holland, 1969). Today, that parasite is eight times as abundant in Puget Sound than it was in the 1940s – an uptick that went entirely unnoticed until our team uncovered it using parasitological dissection of museum specimens (**Figure 2**; Howard et al., in review). If such a large increase in infection can be overlooked, what other disease problems might be quietly increasing?

This example illustrates that parasite abundance can build slowly over time, escaping the notice of observers through a "shifting baselines" effect – the lifetime of any one individual fisher is not long enough to encompass a significant change in parasite abundance, which builds slowly over decades. The increase in infection goes unnoticed until there is an effort to quantitatively compare the abundance of the parasite in the distant past to the present. Our approach – parasitological dissection of museum specimens – is currently the only way to make such a quantitative comparison.

Engagement Strategy

Disseminating results to commercial and subsistence resource users and managers

We will produce both print and digital products aimed at fishers and fishery managers. Our interactive data portal (Gulf of Alaska Fish Parasite Portal) will provide direct access our data. The website will include an interactive map, allowing stakeholders to search, view, plot, and download data in a user-friendly WebGIS interface, including summary information, like the locations of parasite "hot spots" and "cold spots". Links will lead users to information on parasite species, including images for field identification and summaries of potential fishery impacts and links to climate change. We will also produce a brochure that visually summarizes our research findings and encourages use of the data portal. Our print and digital resources will help commercial and subsistence stakeholders make informed choices about where to fish and what species to target. These resources will also help fisheries managers identify parasite species that should be considered in fisheries assessments. We will assess the efficacy of our data portal by tracking unique visitors, time spent on the site, and downloads.

Disseminating results to teachers and students

We propose to create a Data Nuggets (www.datanuggets.org) module to bring real scientific data about parasites to classrooms throughout coastal Alaska (Schultheis and Kjelvik, 2015). We will create a classroom activity that allows students to develop hypotheses and predictions regarding climate change and parasitism, test those predictions with real data, graph their results, and draw conclusions about the future of parasitism in the Gulf of Alaska. Through collaboration with Alaska Sea Grant (ASG) Marine Education Specialist Marilyn Sigman and ASG Marine Advisory Agent Gary Freitag, we will contact science teachers throughout coastal Alaska to encourage their use of this module; we will also work with Lisa Hiruki-Raring (AFSC) to promote our module during Educator Night at AMSS. For a subset of classrooms that use the activity, the graduate student funded by this proposal will arrange to work in-person with students as they complete the Data Nuggets activity. In addition to inclusion in the Data Nuggets database, our module will be listed in a soon-to-be-released, searchable database of “place-based” K–12 educational resources relevant to the Gulf of Alaska on ASG’s Alaska Seas and Watersheds Program website (aswc.seagrant.uaf.edu). Assessment information will be gathered by tracking downloads of the activity from the Data Nuggets and ASG websites, distributing surveys to users of the module, and including a student pre- and post-assessment in materials.

Disseminating results to the interested public

We will conduct pop-up parasite demonstrations in exhibit halls at the UA Museum of the North and the UW Burke Museum, where museum patrons will be able to observe a parasitological dissection of a museum specimen, see parasites through a stereomicroscope, and interact with researchers. These activities will allow us to inform and educate the public about parasites, and will also furnish an opportunity to talk about NPRB, the research it has funded, and the importance of that research.

Links to Prior NPRB Projects Section

Had prior experience with NPRB

no

Project Management

Expertise of team members

Chelsea Wood (Assistant Professor, School of Aquatic and Fishery Sciences, University of Washington) has 13 years of experience in parasitological dissection of marine vertebrates and invertebrates, database management for parasitological data, and statistical analysis of parasitological data. She also has four years of experience in parasitological dissection of liquid-preserved museum specimens. Chelsea has mentored 20 undergraduates, five graduate students, and two post-docs, making her well-qualified to train, supervise, and mentor the graduate student who is chosen to conduct the research described herein.

Luke Tornabene (Curator of Fishes, Burke Museum of Natural History and Culture and Assistant Professor, School of Aquatic and Fishery Sciences, University of Washington) has 12 years of research experience working in natural history collections, including the American Museum of Natural History, the Smithsonian National Museum of Natural History (most diverse fish collection in the world), and the UW Fish Collection (largest collection in the world in total number of specimens). Luke is a classically trained ichthyologist, who has taught three different ichthyology-related courses at UW and Texas A&M University-Corpus Christi and currently mentors nine undergraduates and four graduate students, all of whom are working in the UW Fish Collection. His research interests in Alaska fisheries resulted in his role as PI for the Alaska Fisheries Observer Training program, and his passion for digitization and broader community-utilization of natural history collections led to his involvement as co-PI a NSF grant to digitize 3D CT scans for 30,000 species of vertebrates from US natural history collections.

J Andrés Lopéz (Curator of Ichthyology and Aquatics, University of Alaska Museum of the North and Associate Professor, College of Fisheries and Ocean Sciences, University of Alaska Fairbanks) has 20 years of experience in systematic biology of fishes. He has worked with research collections at the University of Alabama, University of Washington, University of Florida, and Field Museum of Natural History and has served as curator of fishes and marine invertebrates at the University of Alaska Museum for 10 years. In that period the number of holdings in the UA Museum collection has tripled. As an Associate Professor in Fisheries, he leads a research program focused on fish evolutionary biology.

Coordination and collaboration plan

The research proposed herein will be executed primarily by the graduate student to be funded by this grant, who will be enrolled in the Masters program at the School of Aquatic and Fishery Sciences, University of Washington. Chelsea Wood, Luke Tornabene, and J Andrés Lopéz will serve as co-mentors and committee members for this student, with Chelsea Wood serving as the primary advisor. Luke Tornabene will orient the student to the use of natural history collections and will directly supervise this student when he/she is performing fish dissections at the UW Fish Collection. J Andrés Lopéz will directly supervise this student when he/she is performing fish dissections at the University of Alaska Museum of the North. PI Wood will have direct responsibility for the training of the funded graduate student, will manage and ensure data quality, and will assist the graduate student as he/she analyzes the data and writes the three manuscripts that are expected to arise from this project. Alaska Sea Grant's Marine Advisory Program will facilitate connections with coastal Alaskan schools to promote the use of our Data Nuggets classroom activity and coordinate school visits, where the graduate student will directly work with students as they complete that activity.

Luke Tornabene and J Andrés Lopéz agree to the proposed use of specimens outlined in Table 1.

Our team has no other ongoing or submitted grant proposals relevant to this project.

Disseminating results to the marine science community

This work will produce insights about parasitism and climate change that are relevant well beyond the boundaries of the Gulf of Alaska. We will ensure that the marine science community is kept abreast of our findings by writing scientific publications and giving oral presentations of our work in a variety of venues. We expect at least three publications (one from each of the three objectives posed above) to arise from this work, and we will target these publications to high-impact journals, like *Nature Communications*, *Trends in Ecology and Evolution*, and *Ecology Letters*. We will present our work on campus (e.g., departmental seminars at UW and UA), at regional meetings (e.g., Alaska Marine Science Symposium, Disease Working Group of the Puget Sound Ecosystem Monitoring Program), and at national scientific conferences (e.g., the annual meetings of the Ecological Society of America and the American Society of Limnology and Oceanography).

Permits

No permits are required. We have already received approval for the proposed use of specimens outlined in Table 1 from Luke Tornabene (Curator of Fishes, UW Fish Collection) and J Andrés Lopéz (Curator of Ichthyology and Aquatics, University of Alaska Museum of the North).