***Pacific herring (basic introduction)***

Pacific herring (*Clupea pallasii*) are an ecologically and commercially important forage fish with a broad distribution around the Pacific Rim. Populations spawn in the intertidal and upper subtidal zones along the shoreline from southern California to Korea (Haegele and Schweigert 1985; Hay et al. 2008). At each stage of its life cycle, this keystone species directly supports a diverse web of coastal predators including piscivorous fish, marine birds, and marine mammals (Hay 1985; Surma et al. 2018). Humans have harvested Pacific herring for thousands of years and they remain central to cultural and economic relations in coastal indigenous communities (Thornton et al. 2010; McKechnie et al. 2014; Hamada 2015). Commercial fisheries began in the late 1800s when herring were primarily processed into meal for animal food and fertilizer (Reid 1971). Today, most of the commercial harvest is taken in sac roe fisheries (NMFS 2014).

***Pacific herring life cycle and population structure***

Pacific herring in the NE Pacific typically spawn between February and July. Spawning occurs on kelp, eelgrass, and other suitable substrates in intertidal and upper subtidal zones where a single female can produce as much as 20,000 eggs (Hay 1985; Ware 1985). Several weeks after hatching and developing in the water column, larvae metamorphose into juveniles and reside near the shore. Approximately a year after hatching, herring become migratory individuals and join mixed-age schools in open waters, although some populations do not migrate and remain resident individuals (Hay 1985; Beacham et al. 2008). The main recruitment of newly mature individuals occurs in the third year (Stevenson 1962).

Despite a lack of quantitative measures of dispersion and migration back to historical spawning grounds, spatial dynamics of Pacific herring are consistent with a mechanism of learned migration, where recruits learn a migration path from the older fish of the school that they join (Hourston 1982; Petitgas et al. 2006; Byers et al. 2016; Maccall et al. 2019). This mechanism is also consistent with traditional knowledge from long-established aboriginal fisheries (Thornton et al. 2010). Due to this migratory life cycle, population structure in Pacific herring is largely determined by a combination of geographic isolation and local adaptation. However, little is known about mechanisms of reproductive isolation between populations, and post-mating barriers to gene-flow have not been described.

The most prominent structuring within the species is an abrupt genetic discontinuity that occurs between populations separated by the Alaska Pennisula. Surveys of variation in microsatellites, allozymes, and mtDNA show significant divergence between Pacific herring populations in the Bering Sea and the Gulf of Alaska (Grant and Utter 1984; Kobayashi 1993; Liu et al. 2012). Thus, the Alaska Pennisula likely represents a post-glacial contact zone between NW Pacific populations and NE Pacific populations that were previously isolated in southern refugia during late Pleistocene (Liu et al. 2012). Populations within the NW Pacific are genetically similar, with the exception of a population in the Yellow Sea where environmental shifts lead to short-term cycles of extinction and colonization (Hay et al. 2008; Liu et al. 2012). Populations within the NW Pacific are also genetically similar, particularly within the Gulf of Alaska where there is little differentiation between (Seeb et al. 1999; Beacham et al. 2008). There is moderate divergence between Gulf of Alaska populations and southern populations that show spawning-time differences including Cherry Point, Washington and San Fransico Bay, California (Small et al. 2005; Beacham et al. 2008). Generally, these southern populations spawn earlier in the year, show smaller body size, mature more quickly, and have shorter lifespans (Hay et al. 2008).

***Population collapse and lack of recovery in Prince William Sound***

Pacific herring, like other forage fish species, commonly experience periods of population collapse and recovery (Essington et al. 2015; McClatchie et al. 2017; Trochta et al. 2020). Identifying environmental and genetic factors that contribute to these cyclical fluctuations in population size is important to maintain healthy marine ecosystems and manage sustainable fisheries. The Pacific herring population in Prince William Sound (PWS), Alaska experienced a severe collapse that is exceptional among herring populations world-wide (Trochta et al. 2020). The fishery declined from approximately 133 thousand metric tons of spawning biomass in 1988 to 30 thousand metric tons by 1993 and has yet to recover (Pegau 2014). In the Spring of 1989 the Exxon Valdez spilled 11 million gallons of crude oil into PWS. The timing and of this catastrophic event and its devastating impact on local wildlife initially suggested an obvious link between oil exposure and herring population collapse. Indeed, 50% of the egg biomass deposited in 1989 was within the trajectory of spilled oil (Carls et al. 2002) and the contribution of the 1989 year class to the 1993 spawning population was 25% of that forecast (Marty et al. 2003). However, after decades of research, the extent to which the oil spill contributed to the 1993 collapse remains controversial and the lack of recovery after 27 years is largely unexplained (Pearson et al. 1999; Rice and Carls 2007; Thorne and Thomas 2008; Marty et al. 2010; Pegau 2014).

Early post-spill studies funded by Exxon concluded that less than 10% of PWS herring embryos were exposed to damaging concentrations of oil (Pearson et al. 1999). Alternatively, Natural Resource Damage Assessment (NRDA) investigators estimated between 25-52% of embryos could have been negatively affected, citing a lower a threshold of toxicity for polynuclear aromatic hydrocarbons (0.4–0.7 µg·L–1 PAH; (Brown et al. 1996; Carls et al. 2002)). More recent experiments found that herring embryos exposed to an even lower concentration (0.23 µg·L–1 PAH) develop cardiac defects and that 98% of surface water samples collected at PWS during the spawning season of 1989 showed PAH at or above this level (Incardona et al. 2015).

Despite these differing results on the initial effects of oil exposure, industry and government researchers agreed that the oil spill did not likely contribute to population collapse four years later. Instead, it was proposed that a record high herring population faced reduced food availability in the winter of 1991 left the large population stressed and susceptible to disease. The North American strain of viral hemorrhagic septicemia virus (VHSV Type IVa) and the pathogen *Ichthyophonus hoferi* were found tocontribute most to the population decline in 1993 (Meyers et al. 1994; Marty et al. 1998). Epidemiological studies from 1994 to 2002 suggested that the lack of recovery was best explained by low recruitment and high mortality caused by recurring outbreaks of VHSV and *I. hoferi*, but it is unknown why these diseases continue to cycle through the population (Marty et al. 2010). These patterns of low recruitment and high disease prevalence were not observed in the nearby Sitka Sound population, which showed striking synchrony in recruitment from 1980 to 1993 (r2 = 0.95; (Rice and Carls 2007; Marty et al. 2010)). Furthermore, several other nearby populations (Togiak Bay, Craig, Queen Charlotte Islands, and West Vancouver Island) showed strong recruitment events between 1993 and 2005 (Williams and Quinn 2000; Rice and Carls 2007), suggesting that factors limiting recruitment were unique to PWS.

Using microsatellite loci, genetic diversity measured in PWS herring collected in 1995 and 1996 was comparable to that of other healthy Northeast Pacific herring populations in Alaska and British Columbia (O’Connell et al. 1998; Seeb et al. 1999). Furthermore, gene flow seems frequent between southwest PWS and the Gulf of Alaska as well as within the Sound itself (Seeb et al. 1999; Guyon 2006; Roberts et al. 2012).

**Setup for approach**

Using temporal and spatial genomic contrasts to understand the cause of population collapse and lack of recovery.

* Did the oil spill act as a major selective event favoring genetic variation that conferred reduced sensitivity to pollutants?
  + Do we see reduced Ne?
    - Not when Ne is estimated from nucleotide diversity.
    - Perhaps when Ne is inferred from a large drop in the variances in allele frequency changes in PWS
* Is there a lack of genetic diversity in PWS relative to healthy reference populations that may hinder recovery?
  + Not genome-wide. Maybe at key loci.
* Is there a lack of genetic diversity at key loci in PWS relative to healthy reference populations that may hinder recovery?
  + Reduced diversity at genes known to respond to pollution?
  + autocovariance in the allele frequency changes across generations at genes known to respond to pollution?
  + Do we see fixed deleterious variation in PWS?

Adaptation can occur rapidly, but it is difficult to detect in genomic data from a single contemporary timepoint

**Methods**

***Experimental design and sample collection***

***Library preparation, sequencing, and alignment***

Whole genome sequencing of ## individuals resulted in ## raw reads that were trimmed using Cutadapt (v. 1.8.3 (Martin 2011)). Trimmed reads were mapped to the Atlantic herring reference genome (*Clupea harengus* chromosome level genome assembly Ch\_v2.0.2 (Pettersson et al. 2019); chromosomes = 26; total base pairs = 725,670,187; protein coding genes = 24,095; gene transcripts = 67,663) using the Burrows-Wheeler Alignment Tool (v. 0.7.17 (Li and Durbin 2009)). We marked duplicates with Picard Tools MarkDuplicates (v. 2.7.1 (broadinstitute.github.io/picard/)), sorted alignments using Samtools (v.1.9 (Li et al. 2009)), and assessed the quality of alignments with multiQC (Ewels et al. 2016) and Picard Tools CollectWgsMetrics. Mean sequencing coverage was 1.23× across all samples.

***SNP calling and genotype likelihood estimation***

After mapping the reads to the reference genome, we used the Genotype Analysis Toolkit (GATK) to call SNPs and output phred-scaled genotype likelihoods (v. 4.1.4.1 (Poplin et al. 2017)). We generated GVCFs from sorted alignments using Haplotype Caller and followed the GATK4 Best Practice Workflow for variant calling which uses GenomicsDBImport to merge GVCFs from multiple samples. We used GenomicsDBImport to create a database for each of the 26 chromosomes and GenotypeGVCFs to call raw variants across all samples for each chromosome. Raw variants were filtered to include biallelic SNPs at sites with Phred-scaled quality > 20, mapping quality > 30, depth > 600, and depth < 2000. These filtered variants were concatenated into one VCF containing all chromosomes with ‘bcftools concat’ (v. 1.10.2 (Li 2011)). We subset this VCF into 14 VCFs containing samples grouped by population location and year collected, filtered each VCF to include sites with genotyping rate > 50%, and intersected the 14 filtered VCFs with ‘bcftools isec’ to keep sites common across all populations. Finally, we filtered out sites with a minor allele frequency < 0.05. Our final VCF included 204,153 biallelic SNPs. All scripts used to generate the final VCF from raw fastq files are available at (github.com/joemcgirr/pac\_herring).

***Population structure and genome-wide summary statistics***

We converted genotype likelihoods from the final VCF into BEAGLE format and used PCAngsd (Meisner and Albrechtsen 2018) and NGSadmix (Skotte et al. 2013) to analyze population structure. We determined evalAdmix (Garcia-Erill and Albrechtsen 2020). Popvae (Battey et al. 2021).

We used Analysis of Next Generation Sequencing Data software (ANGSD v. 0.931 (Korneliussen et al. 2014)) to calculate within population nucleotide diversity (π), Tajima’s D, relative genetic divergence (Fst), and the population branch statistic (PBS). We subset the final VCF into 14 populations (grouped by location and year collected) and used ANGSD to calculate a folded site frequency spectrum and per site allele frequencies from genotype likelihoods. We used these frequencies to estimated π and Tajima’s D in 50kb sliding windows with a 10kb step size. We created two-dimensional site frequency spectra for each population pair and calculated Fst and PBS in 50kb sliding windows with a 10kb step size. We calculated absolute genetic divergence (Dxy) from allele frequencies output by ANGSD using the CalcDxy.R script in ngsTools (Fumagalli et al. 2014).

***Allele frequency shifts and linkage disequilibrium***

We used ‘bcftools query’ to output allele frequencies for the 14 populations and calculated ∆z, the arcsine transformed allele frequency difference between sampling periods arcsine(sqrt(t1 – t0)). We averaged ∆z in 50kb sliding windows with a 10kb step size.

We used PLINK (v.1.9 (Purcell et al. 2007; Chang et al. 2015)) to estimate linkage disequilibrium (LD) for the 14 populations. We used ‘--indep-pairwise 100 10 0.8’ to calculate r2 (squared allele count correlations).

***Demographic modeling and simulations***

dadi (Gutenkunst et al. 2009) moments (Jouganous et al. 2017)

***Outlier Delimitation***

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