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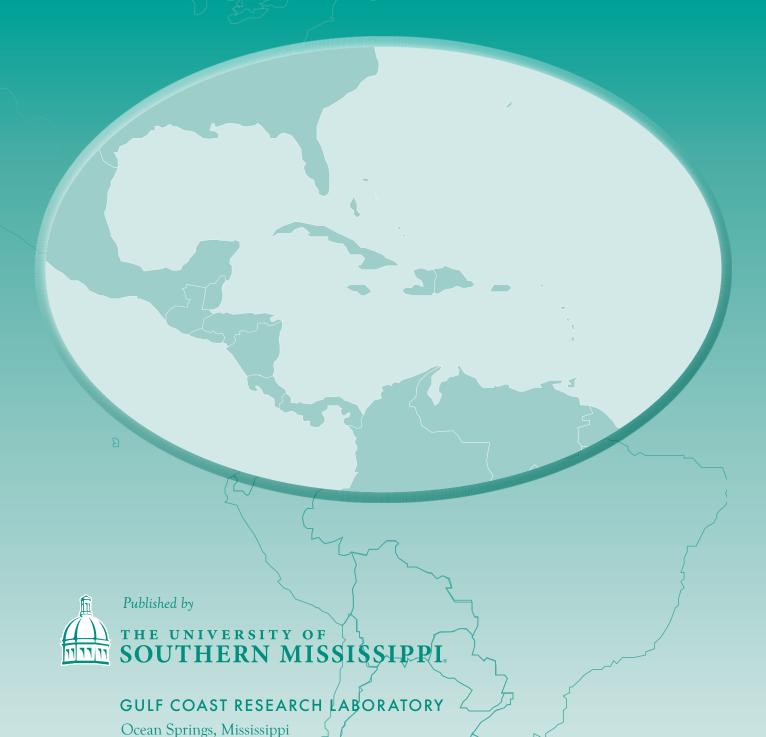
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MULTI—YEAR ENVIRONMENTAL TRENDS OF SHRIMP BLACK GILL (HYALOPHYSA LYNNI) PREVALENCE IN TEXAS GULF COAST SHRIMP POPULATIONS

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ABSTRACT: Shrimp Black Gill, caused by the apostome ciliate Hyalophysa lynni, is an emerging disease impacting penaeid shrimp populations along the southeast Atlantic Coast and the Gulf of Mexico (GOM). Changing annual environmental conditions may drive infection levels of this parasitic ciliate in these populations, which comprise one of the largest fisheries in the United States. Hyalophysa lynni is established on the Texas Gulf Coast, and prevalence of this parasite has a strong seasonal and spatial trend, likely linked with high temperature and a wide range of estuarine salinities. Texas Parks and Wildlife Department monitored shrimp black gill in 2 penaeid shrimp species, Litopenaeus setiferus and Farfantepenaeus aztecus in 2019, with the aim of observing trends in prevalence along spatial and temporal scales. Hyalophysa lynni was found in all 7 bay systems throughout the study period, and this study is a continuation of that monitoring effort, adding 2 years of data collection (2020 and 2021) to prior research. Throughout the entire sampling period (2019–2021) and coastwide, H. lynni was found in 66% of all shrimp samples collected, although prevalence varied annually. Boosted regression tree modeling indicated that low salinity, high temperature, and time of year (late spring through fall) had a significant relationship with H. lynni prevalence in shrimp along the Texas Gulf Coast. Shrimp Black Gill is likely to continue to be present in GOM shrimp populations, and annual precipitation events and increased water temperatures may amplify the population morbidity within any given year.

KEY WORDS: Disease, Penaeid Shrimp, Invertebrate, Estuary, Ecology

Introduction

Shrimp Black Gill (Hyalophysa lynni) is a parasitic ciliate that has been impacting penaeid shrimp populations from the Chesapeake Bay through the Gulf of Mexico (GOM). Hyalophysa lynni has been detected in wild White Shrimp (Litopenaeus setiferus) and Brown Shrimp (Farfantepenaeus aztecus) in the Southeast Atlantic Bight since 1996 (Geer 2003, Gambill et al. 2015, Frischer et al. 2017) and has been confirmed to be present and prolific in both species of penaeid shrimp along the Texas Gulf Coast since at least 2019 (Swinford and Anderson 2021). The symptoms often described as Shrimp Black Gill have only recently been identified as being caused by the parasitic ciliate H. lynni (Landers et al. 2020). It is likely the parasite has been present in the population for much longer as unidentified apostome ciliate cysts. Gill melanization was observed in GOM shrimp as early as the 1970s and had many similarities to visual symptoms caused by H. lynni described in Landers et al. (2020) (Couch 1978, Overstreet 1978, Río-Rodríguez et al. 2013). Research has begun linking the rise in H. *lynni* prevalence with the increase in annual water temperature in recent decades, particularly in the summer, among associated changes in other environmental variables, including salinity and dissolved oxygen (Fowler et al. 2018, Kendrick et al. 2021, Swinford and Anderson 2021). General parasitic prevalence, intensity, and transmission may increase with rising sea surface temperatures associated with climate change (Byers 2021). The combination of these trends indicates that presence of H. lynni may increase in penaeid shrimp populations of the GOM region in the coming decades.

The penaeid shrimp fishery in the GOM is the fifth most profitable fishery in the United States (NMFS 2022). Texas

commercial shrimp landings contribute of up to 26% of the total penaeid shrimp landings in the GOM (NMFS 2022). While shrimp are important commercially, they also serve as a forage species for a great number of predators including Red Drum (Sciaenops ocellatus), Spotted Seatrout (Cynoscion nebulosus), and Southern Flounder (Paralichthys lethostigma), which are important recreational and commercial species (Fujiwara et al. 2016). Hyalophysa lynni was originally thought to correlate with a decline in landings in the southeast Atlantic fishery however, more recent research indicates that there is evidence that H. lynni may not be directly associated with shrimp abundance but instead more closely tied to annual environmental conditions (Frischer et al. 2017, Kendrick et al. 2021). Parasitic prevalence may not be a successful indicator of H. lynni impacts on the fishery, as black gill is an immune response and an indication of survival, not mortality (Kendrick et al. 2021). In the GOM, White Shrimp landings are increasing; however, shrimping is on the decline in this region due to an ever-decreasing profit margin within the fishery (de Mutsert et al. 2008, Keithly and Roberts 2017, Olsen et al. 2021). This pattern suggests that impacts of H. lynni on the fishery may not be immediately observable if other outside factors contribute to declines in shrimping in the region.

Hyalophysa lynni is a parasitic ciliate that imbeds in the gills of penaeid shrimp during a variety of life stages and is speculated to be able to feed on living gill tissue (Landers et al. 2020, Frischer et al. 2022). Successful parasitic infection then induces an immune response from the host shrimp in which the gills produce melanin nodules that encapsulate the ciliate and create cytotoxic quinones that break down attacking cili-

ates (Aguirre-Guzman et al. 2009, Charoensaspri et al. 2014, Frischer et al. 2017, Landers et al. 2020). These cytotoxic quinones can result in the necrosis of both healthy and infected gill tissue (Aguirre-Guzman et al. 2009, Charoensaspri et al. 2014, Frischer et al. 2017). Other species of marine invertebrates, such as other species of penaeid shrimp (Landers et al. 2010; Frischer et al. 2017) including Penaeus monodon (Charoensaspri et al. 2014), caridean shrimp such as Pandalus borealis (Lee et al. 2019), and crabs such as Portunus spinicarpus (Frischer et al. 2022) and Carcinus maenas (White et al. 1985), exhibit similar melanization immune responses that can also result in gill tissue necrosis and are also identified as "black gill" disease. Shrimp infected with H. lynni display significant behavioral changes including a decline in predation avoidance behaviors, and quicker displays of exhaustion behaviors. These changes in behavior may make them more likely to be consumed by major estuarine predators (Frischer et al. 2018, Gooding et al. 2021).

Stressful abiotic conditions (i.e., high temperatures, high salinities, and lowered dissolved oxygen) that are typically indicative of summer months are linked with increased prevalence of *H. lynni* infections (Frischer et al. 2017, Fowler et al. 2018, Kendrick et al. 2021, Swinford and Anderson 2021). These conditions coincide with a seasonal peak in *H. lynni* prevalence during summer and fall in estuaries in the coastal southeastern United States and the GOM (Frischer et al. 2017, Fowler et al. 2018, Swinford and Anderson 2021, Tuckey et al. 2021). Physiological stress induced by changing environmental conditions may only increase parasitic transmission, growth, and survival of *H. lynni* within shrimp populations, and may induce

secondary mortality in a subset of the population (Gooding et al. 2020, Byers et al. 2021, Kendrick et al. 2021). Determining the impact of inter—annual and seasonal variability in environmental conditions on disease prevalence could help predict the impact of *H. lynni* infection on these important ecological and commercial populations.

As environmental conditions change from year to year and annual water temperatures continue to increase on a global scale, *H. lynni* prevalence in the Texas Gulf Coast shrimp population may vary correspondingly, increasing in years with warmer—than—average summer conditions. The goal of this study was to assess prevalence of *H. lynni* in Brown Shrimp and White Shrimp from 2019–2021 in a wide—ranging monitoring study covering 7 bays along the Texas Gulf Coast. This study builds on the preliminary research described in Swinford and Anderson (2021). In addition, effects of environmental and life history variables on disease presence and absence were analyzed to determine potential relationships between environmental variables and prevalence of this disease in Texas over a multiyear period.

MATERIALS AND METHODS Sampling

Samples were collected via trawl or bag seine from 7 Texas bay systems including Sabine Lake, Galveston Bay, East and West Matagorda Bay, Corpus Christi Bay, and the Upper and Lower Laguna Madre (Figure 1). Shrimp were collected monthly from March to November during 2019–2021; 2019 samples were the same as those reported in Swinford and Anderson

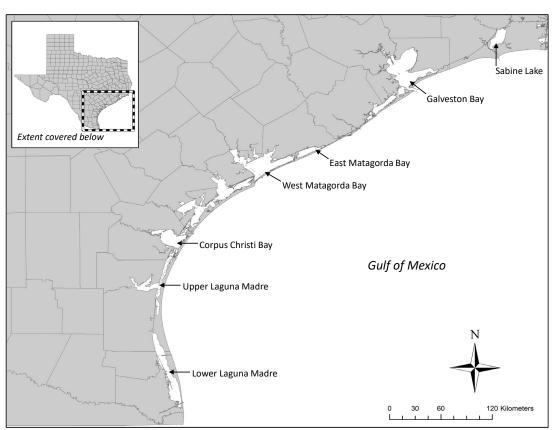


FIGURE 1. Location of bay systems chosen for shrimp sampling along the Texas Gulf Coast, 2019–2021. Sampling locations are the same as in Swinford and Anderson (2021).



FIGURE 2. Four Litopenaeus setiferus displaying the gradient of visual Hyalophysa lynni black gill symptoms, with the bottom shrimp displaying the most severe visual melanization (class 3).

(2021). Samples were collected via the Texas Parks and Wildlife Department (TPWD) Marine Resources Monitoring Program, and the protocols for collection for this survey are detailed in Swinford and Anderson (2021). Visually observed symptoms of H. lynni (black melanized nodules) and a qualitative assessment of symptom intensity for each specimen was also made. Symptom intensity (Figure 2) was categorized by observation of no melanization (0), mild melanization characterized by small patches of melanization, black spots, and light brown or amber color (1), moderate melanization characterized by gills brown or amber in color with black spots more concentrated (2), or high melanization characterized by gills completely black in color (3) (Frischer et al. 2017, Tuckey et al. 2021). Finally, calibrated YSI meters were used to determine mean monthly temperature, salinity, and dissolved oxygen measurements taken with each biological sample during routine sampling (YSI Incorporated, Yellow Springs, OH).

PCR Amplification and Lab Methods

Gill tissue from each shrimp sample was dissected and preserved in 95% ethanol. A Qiagen DNAEasy Blood and Tissue extraction kit was used to extract DNA from preserved gill tissue in accordance with the manufacturer's protocol (Qiagen, Hilden, Germany). The fragment analysis approach described in Swinford and Anderson (2021) was used to validate the taxonomic identity of the ciliate species associated with the symptomatic shrimp. Briefly, the diagnostic PCR assay developed by Frischer et al. (2017) was used to detect *H. lynni*—positive infection, although end—point PCR was performed with the reverse primer fluorescent—labeled for detection on an ABI 3500 DNA sequencer (Life Technologies Corp., Carlsbad, CA), using fragment analysis in the presence of a DNA ladder for size detection. The benefit of this approach was that it enabled precise de-

tection of the correct PCR amplicon size (200 bp) and reduced the probability of amplification and detection of a non—specific product (false positive). This diagnostic assay was used to confirm or reject if shrimp were infected with *H. lynni*, whether they had visually identified symptoms or were asymptomatic. The *H. lynni* PCR assays were run in the presence of 4 serial dilution positive controls (1X concentration, 1:2, 1:10, and 1:100) as well as a single negative control (water of equal volume as DNA aliquots), and infection was diagnosed when a PCR product of the expected size (200 bp) was observed in subsequent gel electrophoresis, with reference to non—amplification in negative control samples. Cycling conditions and more detailed PCR methods can be found in Swinford and Anderson (2021).

Data Analysis

Monthly H. lynni prevalence was calculated as the percentage of total shrimp caught that were confirmed positive with H. lynni utilizing the PCR amplification and fragment analysis sizing protocol. This percentage was calculated for the entire Texas coast, within individual bays, for both species, and for individual years. Differences in infection rates among years were calculated using an analysis of variance (ANOVA) approach. Individuals were aggregated by bay, month, and year, and aggregated infection rates were calculated as the percentage of individuals that tested H. lynni positive (from PCR results) in each bay/month/year combination. A significant ANOVA of infection rate versus year implied differences among years. We examined the results of 4 different variance tests to evaluate the assumption of equal variance among years (O'Brien, Brown-Forsythe, Levene, and Bartlett's tests). Upon finding unequal variances among years in 3 out of 4 tests, a Welch's ANOVA (which does not assume equal variance) was used to measure statistical significance. Qualitative examination of the data distribution suggested that the data were also likely to violate the assumption of normality, but we proceeded based on previous simulations that showed ANOVA is robust to violation of the normality assumption (e.g. Schmider et al. 2010). The ANOVA analysis was performed in the 64-bit version of JMP 14.2 (SAS Institute, Cary, NC).

Percent shrimp with a disease stage (i.e., visual symptoms) was calculated for each stage (0–3), month, and year of the survey. A multiple linear regression was used to determine the significance of month and year on the prevalence of advanced disease stage (classified as stage 2 and 3) within the infected population. Month (modeled as a continuous variable) and year (modeled as a nominal variable) were used to predict the percentage of infected individuals that showed advanced disease stage.

A boosted regression tree approach (BRT) was used to determine the importance of environmental, spatial, and temporal variables on the prevalence of *H. lynni* in sampled shrimp. This method was chosen because a BRT approach is an effective method of working with non–linear relationships, is well suited to address complex multi–variate data, and is robust to multicollinearity between predictor variables (Elith et al. 2008). A cross–validation procedure was used to determine the optimal number of boosting trees, with a Bernoulii error distribu-

tion, tree complexity of 7 nodes, learning rate of 0.01, and bag fraction of 0.5 (Hastie et al. 2001, Elith et al. 2008). Variable input for model selection included month and year sample was collected, species, bay system, sample specimen length (mm), and the water temperature, salinity, and dissolved oxygen upon sample collection. The initial BRT model that included all variables was simplified by backwards stepwise removal of variables that was based on assessment of predictive deviance, with variables dropped when there was no evidence that they improved predictive performance of the model. Partial dependance plots were constructed to assess the final model by fitting a generalized additive model (GAM) spline to the plots of model selected predictor variables against the fitted values of H. lynni prevalence found in shrimp. The BRT analysis was done in R version 3.6.1 (R Core Team 2019), using the package gbm v. 2.1.8 (Ridgeway 2013), and GAMs were fit to the BRT plots utilizing the package mgcv (Wood 2017).

RESULTS

Over the sampling period of 2019–2021, 3,049 of the 4,621 shrimp collected (66%) had gill tissue infected with *H. lynni* based on the presence of a diagnostic PCR amplicon. Monthly shrimp CPUE from long—term TPWD shrimp trawl samples can be found in Supplemental Figure S1. Coastwide prevalence of *H. lynni* peaked in late summer and early fall at 78.8% in August across all 3 years, but prevalence only declined slightly in the following late fall months. While prevalence was still high in late fall coastwide (74.0% in November), early spring prevalence was often low in many of the coastal bay systems (28.2% in March coastwide; Figure 3). When comparing years, 2021

displayed the highest *H. lynni* prevalence (n = 1,606, 75.9%), followed by 2019 (n = 1,605, 64.9%), and then 2020 (n = 1,409, 55.9%). In 2020, sampling did not occur during the months of April and May due to the COVID pandemic, however, *H. lynni* prevalence remained relatively low during the remainder of the sampling period in 2020 in comparison to 2019 and 2021. Prevalence was different across years based on Welch's ANOVA ($F_{2,145} = 7.759$, p = 0.001), and suggested that prevalence was higher in 2021 compared to 2020 and 2019. There was no difference in prevalence between 2020 and 2019. Presence of visual *H. lynni* symptoms (i.e., melanized gill tissue) in shrimp samples was consistently lower (n = 1,880) than *H. lynni* PCR—positive shrimp numbers (n = 3,049; Figure 3).

During the sampling period, 40.7% of sampled shrimp were found to have visual symptoms (gill melanization) of *H. lynni* infection (n = 1,880). Of those with visual symptoms, when classified by disease stage, 60.5 % of shrimp were classified as stage 1 (n = 1,138), 25.3% were classified as stage 2 (n = 475), and 14.2% were classified as stage 3 (n = 267). Overall, advanced disease stage was more common in later months of the year (Figure 4). Among years sampled, 47.9% of shrimp displayed visual symptoms in 2019 (n = 768), 33.9% of shrimp displayed visual symptoms in 2020 (n = 476), and 39.6% of shrimp displayed visual symptoms in 2021 (n = 636). Multiple regression determined that month (moving from spring to winter) had a significant positive correlation with advanced stage (MLR, r^2 = 0.28, $F_{1,23}$ = 6.78, p = 0.0159), but the nominal covariate of year did not.

Throughout the sampling period, the upper coastal bays (Sabine Lake, Galveston Bay, East and West Matagorda Bay) had

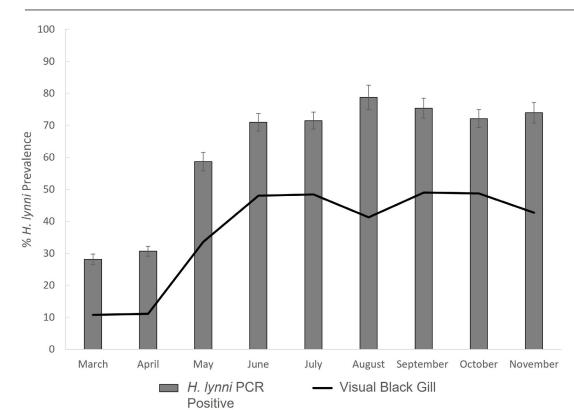


FIGURE 3. Mean (± se) coastwide visual and PCR prevalence of H. lynni over the sampling period of March 2019 to November 2021. Grey bars represent PCR positive H. lynni detected in samples, and the black line represents visual symptoms of H. lynni detected in tissues (blackened melanized gills) (n = 4,621).

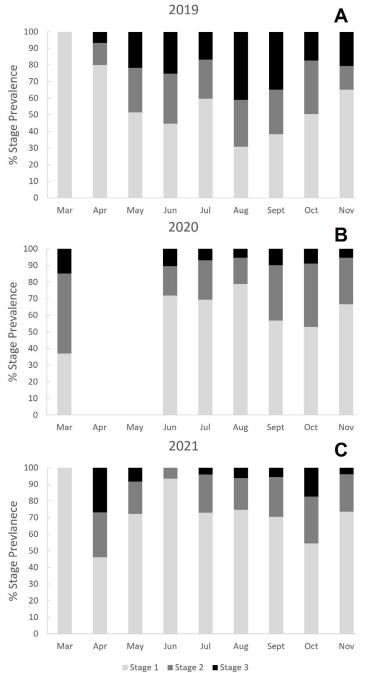


FIGURE 4. Coastwide percentage of H. lynni positive shrimp with visual symptoms by symptom stage in each month and year of the survey. Stage 1, total n = 1,139; Stage 2, total n = 475; Stage 3, total n = 267. A. 2019. B. 2020. Sampling was halted in April and May due to the COVID pandemic and resumed in June. C. 2021.

higher overall disease prevalence for all 3 years compared to the lower coastal bays (Corpus Christi Bay, the Upper and Lower Laguna Madre). Sabine Lake had the highest overall prevalence of *H. lynni* across all 3 years, with 82.1% (n = 692) of shrimp sampled infected, followed by East Matagorda Bay (76.6%, n = 728), Galveston Bay (71.8%, n = 693), West Matagorda Bay (70.5%, n = 695), the Lower Laguna Madre (61.8%, n = 578), the Upper Laguna Madre (49.3%, n = 499), and Corpus Christi Bay (45.1%, n = 736; Figure 5). Of the species sampled coast-

wide during the 3–y sampling period, White Shrimp samples had higher *H. lynni* prevalence at 69.3% (n = 2,509) than Brown Shrimp at 62.1% (n = 2,112). Overall, both Brown and White Shrimp followed the same general seasonal trends, with White Shrimp peaking in *H. lynni* prevalence in September at 78.3% and Brown Shrimp peaking in August at 81.0%.

The BRT model (3,550 trees in the final model) inputs included month, species, year, bay system, length, and water temperature, salinity, and dissolved oxygen upon sampling; however, bay system, dissolved oxygen, species, length, and year were dropped from the BRT during the model simplification step. Summary statistics for water temperature, dissolved oxygen, and salinity associated with shrimp samples for all 3 years during the study period are described in Supplementary Table S1. Salinity explained the highest amount of model deviance in H. lynni prevalence in shrimp (45.8%), followed by month (27.8%) and then closely by temperature (26.5%). Generalized Additive Model outputs indicated that lower salinity (< 10 ppt, Figure 6A), summer and early fall months (Figure 6B), and higher temperatures (> 20°C, Figure 6C) coincided with higher probability and prevalence of H. lynni in shrimp populations of both species.

DISCUSSION

This study reports that *H. lynni* and its associated symptoms were present on the Texas Gulf coast every month throughout the sampling period from 2019–2021. Based on diagnostic PCR, infection was observed in more than half of the collected specimens of both White and Brown Shrimp and was present at some point throughout the sampling period in all 7 bays. In addition, symptom intensity as indicated by a high proportion of advanced disease stages 2 and 3 generally occurred with higher overall disease prevalence, although advanced stages were ob-

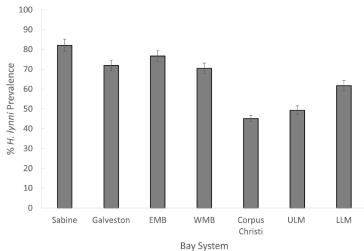
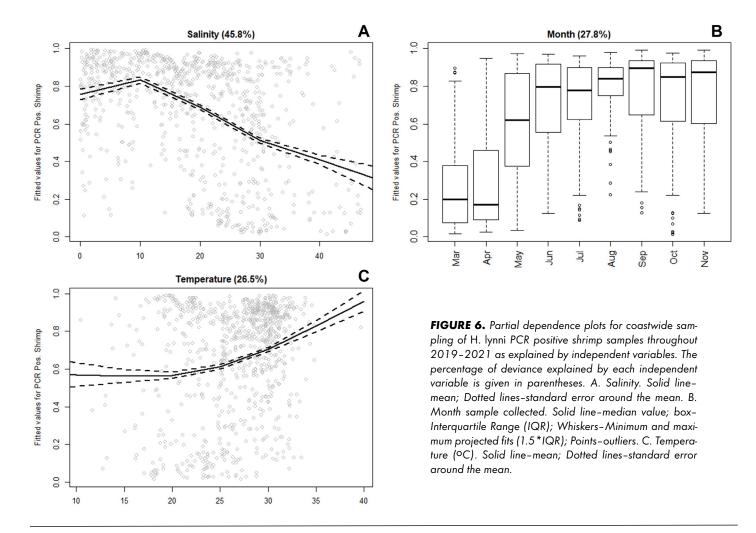


FIGURE 5. Mean (± se) coastwide positive PCR prevalence of H. lynni over the entire sampling period of March 2019 to November 2021 by bay system. Sabine-Sabine Lake, n = 692; Galveston-Galveston Bay, n = 693; EMB-East Matagorda Bay, n = 728; WMB-West Matagorda Bay, n = 695; Corpus Christi-Corpus Christi Bay, n = 736; ULM-Upper Laguna Madre n = 499; LLM- Lower Laguna Madre, n = 578.



served during periods of low disease prevalence as well. Overall, 66.0% shrimp sampled were infected with H. lynni, ranging from 55.9-75.9% annually. Studies on the Atlantic Coast have reported high inter-annual variability in H. lynni prevalence (Frischer et al. 2017, Fowler et al. 2018, Kendrick et al. 2021). Results from this study suggest that long-term H. lynni prevalence in Texas might be greater than even the highest estimates in the Atlantic (e.g., 41%, Kendrick et al. 2021), which may be tied to extended warmer environmental conditions due to the Gulf Coast's lower latitude. Furthermore, PCR diagnosis of H. lynni was consistently higher than diagnosis via visual symptoms (i.e., melanized gill tissue). Prior research in both the GOM and Atlantic demonstrated that PCR is a more robust method for detecting infection (Frischer et al. 2017, Swinford and Anderson 2021), and that reliance on visual diagnosis should only be considered a conservative estimate of H. lynni infection rates.

Variance in prevalence levels from year to year was likely tied to episodic weather events as well as variability in long—term annual water quality conditions such as salinity and temperature. Results from the BRT model indicated that moderate to low salinity, followed by time of year (specifically summer and fall months) and higher temperatures, may drive increased *H. lynni* prevalence in Texas. Mean water temperature in sampling locations remained similar when comparing all 3 years, however

both 2019 and 2021 had lower annual salinity due to higher precipitation during peak H. lynni prevalence (summer and fall) compared to 2020. This may be an indicator of salinity impacting annual variation, as 2020 had consistently higher salinity but suppressed disease prevalence compared to the other 2 years. The annual variation of disease prevalence demonstrates the benefit of ongoing monitoring (Swinford and Anderson 2021) because these variations in H. lynni prevalence may be associated with disparities in key environmental conditions on an annual basis. In preliminary research on the Texas GOM coast, GAM models indicated that only hypersaline conditions (i.e., salinities >35) had a negative impact on H. lynni prevalence (Swinford and Anderson 2021). However, BRT modeling over 3 years from 2019-2021 showed that even salinities >10 can be associated with lower rates of H. lynni prevalence. Evidence from research in the southeast Atlantic indicated that high salinity may be tied to H. lynni prevalence, however, temperature appeared to have a more significant relationship with H. lynni along the Atlantic Coast (Geer 2003, Frischer et al. 2017, Fowler et al. 2018, Kendrick et al. 2021). Salinity regimes in Atlantic versus GOM estuaries can be disparate, and relationships between disease prevalence and the relative importance of environmental variables may vary in different regions (Orlando et al. 1993, 1994; Dame et al. 2000, NOAA 2023). In coastal Texas, northern bay systems (Sabine Lake, Galveston Bay, East and West Matagorda Bay) typically experience higher rainfall and lower salinity conditions than southern bay systems (Corpus Christi Bay, Upper and Lower Laguna Madre), and these conditions seem to be coupled with higher prevalence of *H. lynni* on the upper coast compared to the lower coast. This finding suggests that brackish and low salinity systems in north Texas may be hotspots for this ciliate.

Temperature and month were also important predictors of H. lynni prevalence in the BRT model. Seasonal H. lynni prevalence along the Texas GOM coast generally extended through the full length of the sampling period from March through November, peaking in August or September with mean 78.0-81.0% rates of infection. Prior studies have indicated that peak H. lynni prevalence occurrence is in summer and fall, when high temperature conditions are more common, suggesting an associated relationship between time of year and temperature (Frischer et al. 2017, Fowler et al. 2018, Swinford and Anderson 2021). Prior GAM modeling in Swinford and Anderson (2021) selected temperature as being associated with H. lynni prevalence, although BRT modeling selected time of year as well. Time of year may be a proxy for shrimp abundance in coastal regions as Brown and White post-larval shrimp migrate into estuaries during the spring and summer, and as late as fall in the GOM (Lassuy 1983, Muncy 1984, Olsen et al. 2021). Thus, higher disease prevalence might simply reflect higher abundance of both host species, and simultaneously optimal temperature conditions for post–larval ingress. Monthly shrimp abundance in Texas assessed from long-term TPWD shrimp trawl samples confirms that patterns of increasing abundance

generally pair with seasonal increases of *H. lynni* prevalence, suggesting that shrimp population density itself could be a driver of seasonal prevalence.

Of the variables analyzed in this study, salinity had the tightest relationship to H. lynni occurrence in the Texas GOM coast, with lower salinities driven by precipitation events increasing H. lynni infection levels in shrimp populations. Temperature and time of year may also contribute to H. lynni peaks in late spring through early fall, as water temperatures warm and post larval shrimp are migrating inshore in greater numbers. This research adds to preliminary work done in Swinford and Anderson (2021) by further describing the relationships between H. lynni and environmental attributes along the Gulf Coast. Additional data collection indicated that low salinity and brackish systems may be more vulnerable to the disease and showed that infection in shrimp populations can have significant interannual variability. Hyalophysa lynni prevalence is well established in Texas, and prevalence may be similar throughout the rest of the northern GOM coast. This widespread prevalence may have unprecedented impacts on shrimp populations throughout this region. Annual variability in water quality conditions such as those observed in this study may continue to have unpredictable impacts on H. lynni infection level in any given year. However, long term trends predicted by global climate change scenarios suggest increasing water temperatures and extreme fluctuations in regional precipitation (Thackeray et al. 2022), affecting salinity through river and water diversion. Thus, global climate change effects are likely to elevate *H. lynni* prevalence in GOM coast shrimp populations into the future.

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