Outbreak of eelgrass wasting disease coincides with a protracted marine heat wave

**Authors**

Maya L. Groner1, 2\*, Morgan E. Eisenlord3, Reyn M. Yoshioka4, Evan A. Fiorenza5, Phoebe D. Dawkins5, Olivia J. Graham3, Miranda Winningham3, Alex Vompe6, Natalie D. Rivlin7,8, Bo Yang8, Colleen A. Burge9, Brendan Rappazzo10, Carla P. Gomes10, C.Drew Harvell3

1Prince William Sound Science Center, Cordova, AK 99574, USA

2Affiliate, U. S. Geological Survey Western Fisheries Research Center, Seattle, WA 98115, USA

3Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA

4Oregon Institute of Marine Biology, University of Oregon, Charleston, OR 97420, USA

5Department of Ecology and Evolutionary Biology, University of California Irvine, Irvine, CA 92697, USA

6Department of Microbiology, Oregon State University, Corvallis, OR 97331, USA

7University of British Columbia, Vancouver, BC V6T 1Z1, Canada

8Institute of Marine Environmental Technology, University of Maryland Baltimore County, Baltimore, MD 21202, USA

9Department of Sociology, University of Central Florida, Orlando, FL 32816, USA

10Department of Computer Science, Cornell University, Ithaca, NY 14853, USA

\*Corresponding author: mgroner@pwssc.org

**Running title:** Eelgrass disease and marine heat wave

**Abstract**

Marine heat waves are increasing in occurrence, severity, and duration, with unquantified impacts on species interactions, including disease. The impacts of prolonged temperature stress on host-pathogen interactions are not well explored. We correlated mid-summer prevalence of eelgrass wasting disease (EWD) with remotely sensed seawater temperature metrics before, during and after the 2015-2016 marine heat wave in the northeast Pacific, the longest marine heat wave in recent history. EWD prevalence ranged between 5-70% in 2013 and increased to 60-90% by 2017. EWD severity approximately doubled each year between 2015 and 2017. Shoot density declined by 60% shortly after the heat wave began and did not rebound. EWD prevalence was correlated with warmer winter and spring temperatures while EWD severity was correlated with warmer winter temperatures. We hypothesize that the association of increased disease with warming conditions results from changes in both the timing of the seasonal disease cycle and an increase in the growth rate of *Labyrinthula zosterae,* the etiologic agent of EWD,at warmer temperatures. The association between increased summer EWD and prior winter and spring temperatures suggests that heat waves accelerate EWD outbreaks and that seawater temperature has potential to be utilized as an early warning system for EWD.

Keywords: *Labyrinthulomycetes, seagrass, opportunistic pathogens, marine disease, warm water anomaly, heat wave, Heterokont*

1. **INTRODUCTION**

Marine disease outbreaks are frequently linked to short-term changes in temperature (Burge & Hershberger 2020), while impacts of long-term warming on disease, particularly marine heat waves are less well explored (Harvell et al. 2019; Burge & Hershberger 2020). This is likely because few long-term datasets on disease prevalence in the oceans exist, and recognition of heat waves as an important oceanographic phenomenon is recent, having only received a technical definition in 2016 (Hobday et al. 2016). Heat waves, which occur when seawater temperature exceed a threshold (usually the 90th percentile) of seasonally varying averaged temperatures for at least five consecutive days) are increasing in severity, duration, and intensity (Hobday et al. 2016, Oliver et al. 2018). Impacts from the longest heat wave described to date, which occurred in the northeast Pacific Ocean from 2014-2016, include mass mortality of planktivorous seabirds, widespread harmful algal blooms, changes in plankton productivity and composition and an outbreak of seastar wasting disease in numerous species including the sunflower star (*Pycnopodia helianthoides*), a keystone predator (Cavole et al. 2016, Gentemann et al. 2017, Harvell et al. 2019). These examples demonstrate that heatwaves can have dramatic and lasting ecosystem impacts, and underly the critical need to understand how these prolonged stressors alter host-pathogen interactions.

Disease outbreaks can be particularly damaging when they affect ecosystem engineers such as corals, oysters, and seagrasses (Burge and Hershberger 2020). In seagrasses, wasting disease is one of myriad stressors associated with global population declines (Waycott et al. 2009, Martin et al. 2016, Sullivan et al. 2018). The largest known outbreak of wasting disease occurred in the 1930’s along the European and North American coastlines of the Atlantic Ocean (Renn 1936). During this outbreak, eelgrass (*Zostera marina*) meadows suffered up to 90% mortality. Impacts of the outbreak include altered sediment distribution, disrupted coastal food chains, fisheries, and migratory waterfowl (Short et al. 1988). In recent years, the dominant temperate seagrass of the northern hemisphere, eelgrass, has declined in critical estuaries on both the US Atlantic and Pacific coasts (Lefcheck et al. 2017, Harenčár et al. 2018). The degradation of these complex ecosystems has multiple, poorly understood causes. Although disease testing is rarely done, EWD outbreaks and elevated temperatures are hypothesized to be contributing to recent eelgrass declines in North America (Groner et al. 2014, Martin et al. 2016, Lefcheck et al. 2017, Harenčár et al. 2018, Sullivan et al. 2018).

EWD is caused by an opportunistic pathogen, *Labyrinthula zosterae* (*Lz*), that falls within the Labyrinthulomycetes (Muehlstein et al. 1991). *Lz* causes intracellular infections in leaf tissue, where it moves along a secreted mucus network to spread. Disease signs include black or brown lesions with defined borders and, often, a white necrotic center (Muehlstein et al. 1991). *Lz* is sensitive to environmental conditions, including warming temperatures (Dawkins et al. 2018, Brackel et al. 2019). Long-term studies (e.g., Bull et al. 2012) are needed to understand the full effect of temperature on EWD in the field and determine potential drivers of outbreaks. Recent studies have correlated heatwaves to substantial seagrass die-offs (Strydom et al. 2020), reduced restoration success (Aoki et al. 2020), and changes in fatty acid composition (Beca-Carretero et al. 2018); however, little is known about seasonal and multi-years patterns in prevalence and severity, impacts of wasting disease on populations, or the role of temperature in facilitating outbreaks (Bull et al. 2012, Groner et al. 2014, 2016, Dawkins et al. 2018, Sullivan et al. 2018, Brakel et al. 2019).

To further investigate the association between EWD and ocean warming, we surveyed eelgrass health at nine sites in the San Juan Islands, WA, USA spanning the years prior to, during, and after the 2014-2016 heat wave in the Northeast Pacific. Frequently called ‘the blob’, this heat wave was unprecedented in duration, intensity, and geographic scale. It was driven by both warm surface waters combined with unusually weak coastal winds that hindered upwelling events (Gentemann et al. 2017). We quantified patterns of mid-summer EWD prevalence and severity in the San Juan Islands from 2013-2017 and identified correlations between remotely sensed seawater temperatures and field measurements of EWD prevalence, EWD severity and eelgrass shoot density. To understand the association between Lz and EWD lesion, we quantified *Lz* infection loads in and adjacent to EWD lesions in field-collected plants.

1. **LITERATURE CITED**

Aoki LR, McGlathery KJ, Wiberg PL, Al-Haj A (2020) Depth Affects Seagrass Restoration Success and Resilience to Marine Heat Wave Disturbance. Estuaries Coast 43:316-328

Beca-Carretero P, Guihéneuf F, Marín-Guirao L, Bernardeau-Esteller J, García-Muñoz R, Stengel DB, Ruiz JM (2018) Effects of an experimental heat wave on fatty acid composition in two Mediterranean seagrass species. Mar Pollut Bull 134:27-37

Brakel J, Jakobsson-Thor S, Bockelmann AC, Reusch TB (2019) Modulation of the Eelgrass–*Labyrinthula zosterae* Interaction Under Predicted Ocean Warming, Salinity Change and Light Limitation. Front Mar Sci 6:268

Bull JC, Kenyon EJ, Cook KJ (2012) Wasting disease regulates long-term population dynamics in a threatened seagrass. Oecologia 169:135-142

Burge CA, Hershberger PK (2020) Climate change can drive marine diseases. In: DC Behringer, BR Silliman, KD Lafferty (Eds.), Marine Disease Ecology (pp. 83-94). Oxford University Press, New York

Caldwell JM, Heron SF, Eakin EM, Donahue MJ (2016) Satellite SST-based coral disease outbreak predictions for the Hawaiian Archipelago. Remote Sens 8:93

Cavole LM, Demko AM, Diner RE, Giddings A, Koester I, Pagniello CM, Paulsen ML, Ramirez-Valdez A, Schwenck SM, Yen NK, Zill ME (2016) Biological impacts of the 2013–2015 warm-water anomaly in the Northeast Pacific: winners, losers, and the future. Oceanography 2:273-285

Dawkins PD, Eisenlord ME, Yoshioka RM, Fiorenza E, Fruchter S, Giammona F, Winningham M, Harvell CD (2018) Environment, dosage, and pathogen isolate moderate virulence in eelgrass wasting disease. Dis Aquat Org 130:51–63

Gentemann CL, Fewings MR, García‐Reyes M (2017) Satellite sea surface temperatures along the West Coast of the United States during the 2014–2016 northeast Pacific marine heat wave. Geophys Res Lett 44:312-319

Groner ML, Burge CA, Couch CS, Kim CJ, Siegmund GF, Singhal S, Smoot SC, Jarrell A, Gaydos JK, Harvell CD, Wyllie-Echeverria S (2014) Host demography influences the prevalence and severity of eelgrass wasting disease. Dis Aquat Org 108:165-175

Groner ML, Burge CA, Kim CJ, Rees EE, Van Alstyne KL, Yang S, Wyllie-Echeverria S, Harvell CD (2016) Plant characteristics associated with widespread variation in eelgrass wasting disease. Dis Aquat Org  118:159-168

Groner ML, Burge CA, Cox R, Rivlin ND, Turner M, Van Alstyne KL, Wyllie-Echeverria S, Bucci J, Staudigel P, Friedman CS. (2018a) Oysters and eelgrass: Potential partners in a high pCO2 ocean*.*Ecology 99:1802-1814

Groner ML, Shields JD, Landers Jr DF, Swenarton J, Hoenig JM (2018b) Rising temperatures, molting phenology, and epizootic shell disease in the American lobster. Am Nat 192:E163-E177

Harvell CD, Montecino-Latorre D, Caldwell JM, Burt JM, Bosley K, Keller A, Heron SF, Salomon SF, Lee L, Pontier O, Pattengill-Semmens C (2019) Disease epidemic and a marine heat wave are associated with the continental-scale collapse of a pivotal predator (*Pycnopodia helianthoides*). Science advances 5:p.eaau7042

Hobday AJ, Alexander LV, Perkins SE, Smale DA, Straub SC, Oliver EC, Benthuysen JA, Burrows MT, Donat M, Feng M, Holbrooke N (2016) A hierarchical approach to defining marine heatwaves. Prog Oceanogr 141:227-238

Lefcheck JS, Wilcox DJ, Murphy RR, Marion SR, Orth RJ (2017) Multiple stressors threaten the imperiled coastal foundation species eelgrass (*Zostera marina*) in Chesapeake Bay, USA. Glob Change Biol 23:3474-3483

Martin DL, Chiari Y, Boone E, Sherman TD, Ross C, Wyllie-Echeverria S, Gaydos, JK, Boettcher AA (2016) Functional, phylogenetic and host-geographic signatures of *Labyrinthula* spp. provide for putative species delimitation and a global-scale view of seagrass wasting disease. Estuar Coasts 39:1403-1421

Muehlstein L, Porter D, Short F (1991) *Labyrinthula zosterae* sp. nov., the causative agent of wasting disease of eelgrass, *Zostera marina*. Mycologia 83:180–191

Oliver EC, Donat MG, Burrows MT, Moore PJ, Smale DA, Alexander LV, Benthuysen JA, Feng M, Gupta AS, Hobday AJ, Holbrook NJ (2018) Longer and more frequent marine heatwaves over the past century. Nat Commun 9:1-12

Renn CE (1936) The Wasting Disease of *Zostera marina*. I. A Phytological investigation of the diseased plant. Biological Bulletin 70:148-158

Short FT, Ibelings BW, Den Hartog C (1988) Comparison of a current eelgrass disease to the wasting disease in the 1930s. Aquat Bot 30:295-304

Strydom S, Murray K, Wilson S, Huntley B, Rule M, Heithaus M, Bessey C, Kendrick GA, Burkholder D, Fraser MW, Zdunic K (2020) Too hot to handle: unprecedented seagrass death driven by marine heatwave in a World Heritage Area. Glob Change Biol 26:3525-3538

Sullivan BK, Trevathan-Tackett SM, Neuhauser S, Govers LL (2018) Host-pathogen dynamics of seagrass diseases under future global change. Mar Pollut Bull 134:75-88

Waycott M, Duarte CM, Carruthers TJ, Orth RJ, Dennison WC, Olyarnik S, Calladine A, Fourqurean JW, Heck KL, Hughes RA, Kendrick GA (2009) Accelerating loss of seagrasses across the globe threatens coastal ecosystems.  Proc Natl Acad Sci USA 106:12377-12381