MICROBES AND AIRPLANES: INVESTIGATING MICROBIOLOGICALLY-INFLUENCED CORROSION OF SUBMERGED WORLD WAR II AIRCRAFT WRECK SITES

By

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ABSTRACT

There is perhaps no better symbol of the destruction, technological advancement, and geographical scale of World War II than aircraft. Today, thousands of these wartime vestiges are located beneath the ocean's surface, serving as a highly sought after form of material culture. While archaeologists tend to opt for in situ preservation strategies, there are those who have advocated for a different 'preferred' option, instead promoting recovery. Proponents of the latter perspective have levied charges of inaction against archaeologists, citing unchecked degradation as the impetus for salvaging submerged aircraft wreck sites. To counter these claims, and better understand the degradative forces that place these sites at risk, the totality of environmental factors needs to be comprehensively assessed. This includes a site's microbiome, as previous research has indicated that colonizing microorganisms have the potential to detrimentally impact steel shipwreck sites and other forms of underwater cultural heritage. However, aluminum aircraft of World War II have yet to be the focus of similar investigations, leaving a void in the field's understanding regarding in situ preservation threats. Thus, this dissertation is the first attempt to extend this line of research to submerged aircraft wreck sites, using four sites in Hawai‘i. The first step involves characterizing the microbes present, which necessitated sound

collection protocols for obtaining microbial samples. The methodology developed for this project was designed to be practical, affordable, and amenable to a variety of uses. The successful collection of biofilm, the main form of biofouling on submerged aircraft wreck sites, enabled DNA sequencing of the material from these samples. The sequencing results allowed for an interpretation of the microbial assemblages associated with corroded and non-corroded wreck surfaces. While no significant taxonomic differences were identified between corroded and non-corroded samples, the study succeeded in defining the microbial communities of submerged aircraft wreck site biofilm, which appeared compositionally-distinct from those of the surrounding seawater and sediment. In addition to identifying key constituents, the data indicated that environmental factors, including the background microbiome and sedimentary interactions, play a prominent role in shaping submerged aircraft wreck site biofilms. Ultimately, evidence of microbiologically-influenced corrosion of submerged aircraft wreck sites remains inconclusive, although significant strides were made in understanding the microbial communities associated with these sites. For archaeological management, the study provides a sound methodology for future collections, baseline data, and the identification of necessary approaches and additional lines of evidence. There is an inherent value in being the first to attempt to see what works, thus serving as a launching point for future, more sophisticated forms of analyses that strive towards developing definitive statements on the relevancy of microbiologically-influenced corrosion to the in situ preservation of submerged aircraft wreck sites.

Microbes and Airplanes: Investigating Microbiologically-Influenced Corrosion of Submerged World War II Aircraft Wreck Sites

A Dissertation

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ACRONYMS

3D	Three Dimensional
A&T	A&T Recovery
ANOSIM	Analysis of Similarities
CNMI	Commonwealth of the Northern Marianas Islands
DBEDT	Department of Business, Economic Development and Tourism
DIN	Dissolved Inorganic Nitrogen
DNA	Deoxyribonucleic Acid
DOD	Department of Defense
DON	Department of the Navy
DPAA	Department of POW/MIA Accounting Agency
ECAC	European Civil Aviation Conference
E_{corr}	Corrosion Potential
ECU	East Carolina University
eDNA	Environmental (or Extracellular) Deoxyribonucleic Acid
EPS	Extracellular Polymeric Substances
FeOB	Iron-Oxidizing Bacteria
FLAM	Flying Leatherneck Aviation Museum
FOIA	Freedom of Information Act
GDP	Gross Domestic Product
GOM	Gulf of Mexico
HAB	Harmful Algal Bloom
HTA	Hawaiʻi Tourism Authority
HUD	Department of Housing and Urban Development
ILSCR	Inventory List of Submerged Cultural Resources
IMR	Integrated Microbiome Resource
MAM	Military Aviation Museum
MHP	Maritime Heritage Program
MIC	Microbiologically-Influenced Corrosion
MOA	Memoranda of Agreement
NAS	Naval Air Station
NERD	Naval Exploration and Research Divers
NFT	Non-Fungible Token
NHHC	Naval Heritage and History Command
NHPA	National Historic Preservation Act
NMDS	Non-Metric Multidimensional Scaling
NMS	National Marine Sanctuary
NNAM	National Naval Aviation Museum
NOAA	National Oceanic and Atmospheric Administration
NPS	National Park Service
NRHP	National Register of Historic Places
NTEP	Navy Trade and Exchange Program
OMNS	Office of National Marine Sanctuaries
OSC	Office of Statistical Control
OTU	Operational Taxonomic Unit
pCO_2	Carbon Dioxide Partial Pressure

PHAM	Pearl Harbor Aviation Museum
PNG	Papua New Guinea
RNA	Ribonucleic Acid
ROV	Remote Operated Vehicle
SAWS	Submerged Aircraft Wreck Site
SCUBA	Self-Contained Underwater Breathing Apparatus
SEM	Scanning Electron Microscopy
SFP	Site Formation Process
SHA	Society for Historical Archaeology
SHPD	State Historic Preservation Division
SIMPER	Similarity Percentage
SMCA	Sunken Military Craft Act
SRB	Sulfate-Reducing Bacteria
TIGHAR	The International Group for Historic Aircraft Recovery
UAB	Underwater Archaeology Branch
UCH	Underwater Cultural Heritage
UH	University of Hawai‘i, Mānoa
UN	United Nations
UNESCO	United Nations Educational, Scientific and Cultural Organization
US	United States
USAAF	United States Army Air Forces
USAF	United States Air Force
USC	United States Code
USD	United States Dollar
USN	United States Navy
VLR	Very Long Range
WWII	World War II

Chapter 1: Introduction

Project Context

In 2001, maritime archaeologists from around the world came out in support of the UNESCO *Convention on the Protection of Underwater Cultural Heritage* (UNESCO 2001a). While the details of how said protection should proceed and what constitutes 'underwater cultural heritage' (UCH) have since been debated (Bederman 1999; Browne and Raff 2023; Dromgoole 2010; Forrest 2002; Khakzad 2014a, 2014b; Lanciotti 2021; Maarleveld 2007; O'Keefe 2013; Perez-Alvaro 2019; Sarid 2017; Secci and Spanu 2015; Staniforth et al. 2009; Strati 2006; Guérin and Barbara Egger 2010), there is a general consensus amongst the field's practitioners that the preservation of submerged material culture is a worthwhile endeavor. Supporting the continued existence of archaeological sites has been framed as a public good that benefits a range of stakeholders (Comer 2014; Green et al. 2021; Little and Shackel 2016; Martin 2021; Sable and Kling 2001; Scott-Ireton 2020; Serageldin 1999; Viduka 2021). The tangible heritage beneath the ocean surface represents a vast continuum of human interactions, some of which are foundational aspects of national and cultural identities. Archaeologists, who are often tasked with the stewardship of these historical vestiges, have largely abandoned the mentality that the only way to preserve UCH is through recovery and placement in a museum. Instead, in situ preservation has traditionally been touted as the 'preferred' option (Babits and Van Tilburg 1998; Bergstrand and Nyström Godfrey 2007; Broadwater and Nutley 2009; Manders 2008), while the Annex to the 2001 Convention listed in situ preservation as the 'first option' (Anzar 2018; UNESCO 2001b).

Neither new, nor radical, in situ preservation is now largely accepted as the standard within professional archaeology (Bulut and Yüceer 2023; Calantropio and Chiabrando 2023;

Maarleved 2020; Ricca and La Russa 2020). Justifications for this site management strategy are primarily vested in notions of stakeholder access and maintaining the original historic context, as well as more practical considerations regarding the logistics and resources involved with recovery operations and artifact conservation (Chen et al. 2022; Gregory 2009; Gregory et al. 2012; Khakzad and Van Balen 2012; Maarleveld et al. 2013; Manders et al. 2011; Ortmann et al. 2010; Richards 2011; Riera et al. 2016). The concurrence of accepting the responsibility of site management and a shift towards the in situ preservation ethos has spurred a deluge of research dedicated to understanding various impacts that threaten a site's physical status (Brennan et al. 2013; Brennan 2016; Damour et al. 2016; Edney 2016; Fernández-Montblanc et al. 2022; Firth 2018; Nyström Godfrey et al. 2012; MacLeod 2002, 2016; Moore 2015). Research articles and studies that aim to characterize these natural and anthropogenic factors are viewed as equally valid as more traditional pursuits related to site discovery, documentation, and interpretation. This sentiment was recently affirmed during discussions regarding the role of maritime heritage within the United Nation's (UN) Decade (2021-2030) of Ocean Science Initiative (Henderson, 2019; Lee, 2019; Trakadas et al., 2019).

Identification of possible threats and empirically assessed impacts provide site managers with key information on which management and mitigation strategies are advisable. Among the in situ preservation threats that have been studied by underwater archaeologists, corrosion has arguably garnered the most attention (MacLeod 2002; Moore 2015). Here, corrosion is in reference to the "destructive attack of a metal by its reaction with the environment" (McCafferty 2010:1), and thus, only applicable to metallic forms of UCH. The corrosion process is an element-specific reaction, meaning that the form and extent of corrosion products is dependent on the primary metal and any alloying constituents. As such, much of the literature in maritime archaeology and cultural resource management has been dedicated to the study of iron oxidation in marine environments, given the role iron, and later steel, has played in shipbuilding since the advent of ironclad warships in the early 19th century (Thiesen 2000). The emphasis on iron corrosion impacts to UCH, particularly for western maritime nations, is, in part, due to World War II (WWII). This global conflict may be the single largest event responsible for the deposition of material culture into the ocean, with steel shipwrecks serving as both the archetypal site and a significant component of submerged cultural resource inventories. The historic significance of the war, combined with its temporal recency, has imbued sites from this era with a particularly heightened societal importance, which generates demand for both site access and preservation (Edney 2018; Jeffery 2007; McKinnon 2013; Panakera 2007). Of course, these sentiments are not only applicable to combat ships, landing craft, and freighters made of steel, but extend to the hallmark symbol of WWII: aircraft.

The sheer quantity of air traffic during the war resulted in tens of thousands of aircraft being deposited into the world's oceans. This proliferation means that submerged aircraft wreck sites (SAWSs) are by no means a niche subcategory of UCH, but instead, a frequently encountered site type whose wartime role attracts a variety of site visitors. Once wrecked in the water, the aluminum-based planes were subjected to the same corrosive forces that are responsible for transforming steel into oxidized rust. Yet, aluminum does not corrode in the same fashion as iron (Berzins et al. 1977; Davis 1999; Dix et al. 1975; Goodard et al. 1967; MacLeod 1983). The consideration of site formation processes (SFPs) relevant to aircraft must then account for these metallurgic differences (Bell 2010). In 2006, the first known corrosion survey of WWII planes was conducted in Chuuk Lagoon, which provided valuable insights into how the ambient seawater can both contribute and compromise site preservation (MacLeod 2006). Since then, additional monitoring efforts have revealed a complex picture for the corrosion of aircraft wreck sites in aquatic contexts (Lickliter-Mundon and Leverenz 2023; Richards and Carpenter 2012, 2018). Identified contributors to this process include chemical reactions at the metal-seawater interface, differential corrosion rates owing to various metal alloys in contact with one another (i.e. galvanic corrosion), and fluctuations in site exposure to dissolved oxygen due to currents and extreme weather events.

While this information has been critical in understanding how SAWS in situ preservation is impacted by continued submergence, there has not been any consideration of the effects that the marine biota, specifically microorganisms, have on site degradation. Biofouling on SAWSs is primarily defined by thin microbial biofilms that form as a result of bacterial colonization on the surface. Research from outside the fields of historic preservation and maritime archaeology have unveiled numerous instances of increased corrosion associated with marine biofilms, including microbial activity directly impacting various aluminum alloys (Abdoli et al. 2016; Jaume et al. 2023; Maciel et al. 2019; Pratikno and Titah 2017; Zhang et al. 2019, 2022). This phenomenon of microbes altering the microenvironmental conditions of a metal substrate, leading to enhanced corrosion has been dubbed microbiologically-influenced corrosion (MIC). Though MIC has yet to be assessed in terms of its relevancy to SAWSs, an array of other UCH materials, primarily made of iron and steel, have been the subject of research efforts intended to discern the extent and causes of MIC (Albahri et al. 2019; Chock and Silva 2016; Church et al. 2007; Cullimore and Johnston 2008; Cybulska et al. 2020; Damour et al. 2016; De Baere et al. 2019, 2021; Little et al. 2019; MacLeod et al. 2017; Mugge et al. 2019a; Price et al. 2021; Salazar and Little 2017; Usher et al. 2014; Van Landuyt et al. 2022). Spurred by a greater recognition of the overall ecology associated with underwater archaeological resources, microbiomes are now regularly being considered in evaluations of in situ preservation (May et al. 2008; Nyström Godfrey et al. 2012; Paxton et al. 2024). Thus, this dissertation represents an attempt to extend that line of thinking to SAWSs and encourage heritage professionals to take a more critical approach to the management of this site type.

The following study is intended to be an interdisciplinary exercise, where the archaeological and anthropological context of SAWSs is used to justify the investment in research pertaining to in situ preservation. In turn, that research involves the utilization of methods from the biological and chemical sciences in order to analyze microbial biofilm communities gathered from four WWII-era SAWSs off the coast of Hawaiʻi. The interpretation of the results, which were generated using DNA sequencing for taxonomic identifications, is guided by a desire to further the archaeological field's understanding of how MIC may be contributing to SAWS degradation. While the data may be of inherent interest from an ecological standpoint, its relevance to UCH management must be made explicit for this dissertation to truly be interdisciplinary. By doing so, MIC can be properly contextualized within the web of SFPs that affect SAWSs, allowing resource managers to better prioritize responses to specific in situ preservation threats (Pruitt and McKinnon 2024). That said, the integration of 'hard' science approaches to answering questions fundamentally concerned with historic preservation should not be lauded, but instead, be the expected standard. This does not mean that archaeologists should become experts in microbiology and/or electrochemistry, the two disciplines most germane to MIC. Rather, there should be an expectation that those entrusted with site management are able to identify how non-archaeological data can also be used to best formulate strategies and recommendations regarding in situ preservation. Conversely, the sampling and analysis procedures developed for the current study are an attempt at formulating a standardized methodology that may have applications beyond historic preservation, as discussed later in this dissertation.

Finally, before moving on to an explanation of how this dissertation is laid out, it should be mentioned that much of the content is written from the perspective of historic preservation practices in the United States (US). While WWII SAWSs are globally dispersed, the selection of four sites within US waters, all of which are associated with the US military, encouraged the domestic focus. Thus, the interpretations of the study results are generally applicable to SAWSs regardless of geography, though the legal framework and cultural significance guiding this effort may be irrelevant in other locations. Furthermore, SAWS management is largely being conceptualized from the standpoint of relevance to government management agencies, specifically those in Hawaiʻi. This was done to maximize the utility of the microbiological data for archaeological management, illustrating real-world applications of the research. Additionally, this research was largely supported by a grant from the National Park Service's (NPS) National Center for Preservation Technology and Training, a federal government research center "dedicated to advancing the field of historic preservation through the use of science and technology."[1]

As such, there is limited discussion pertaining to the complicated cultural significance of SAWSs through their connection to WWII. For Hawaiʻi, the war had a profound effect on the island communities, with a legacy that still impacts the current population (Abe and Imamura 2019; Coffman 2003; Creighton 1978; Edwards et al. 2016; Loague et al. 1996; Niheu et al. 2007). The aircraft that now represent this transformative and tumultuous period of Hawaiian history likely evoke emotions different from those related to national pride and sacrifice that are

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[1] https://www.nps.gov/subjects/ncptt/index.htm

traditionally ascribed to these sites (Daly 2018; Dechow and Leahy 2010; Fix 2011; Jeffery 2007; Marter et al. 2017; Wayland 2006). A WWII wrecked aircraft is not exclusively under the domain of US military history, but as Marter et al. (2017:42) states, "its departure from one place and its crash…in another weaves a link between the two places. It now resides both physically and spiritually within a new community that has adopted it into 'their story'." Interpretation of that story is, of course, highly dependent on cultural considerations. Resentment towards militaristic material culture may also be spurred by an association between the US military's presence and the illegal annexation of Hawaiʻi in 1898, as well as the colonial period and statehood admission that followed (Blackford 2004; Budnick 1992; Dudley 1993; Herman 1999; Kameʻeleihiwa 1992; Kauanui 2018; Silva 2004; Whitehead 1993). While there is an explicit recognition that some may not wish for SAWSs to be preserved because of the US government's impact on indigenous sovereignty, further examination of contested heritage remains outside the scope of the project objectives. There are, however, many excellent discussions that address pluralistic views on WWII heritage in the Pacific and the difficult conversations these ignite (Jeffery 2007; MacDonald 2015; McKinnon 2013; McKinnon et al. 2019; Poyer et al. 2000; Price et al. 2013; Raffield et al. 2023).

Dissertation Layout

The remainder of Chapter 1 provides the necessary context for the microbiological sampling and analysis efforts used to elucidate information on the relevancy of MIC to SAWS preservation. This begins with a description of SAWSs as heritage resources, including their representation in the Hawaiian submerged cultural landscape and an overview of the cultural significance that justifies their protection. The relevant management agencies are then identified before introducing the concept of in situ preservation as it relates to SAWSs. An argument for the appropriateness of this site management strategy is made primarily on the basis of the non-consumptive uses that in situ preservation promotes. These forms of site interactions have the potential to yield considerable economic benefits related to recreational wreck diving and the wider heritage tourism industry. The benefits of in situ preservation are contrasted with the detrimental effects of recovery, thus inviting a discussion on the methods available to site managers who opt against removing SAWSs from the seafloor. While stabilization techniques are briefly mentioned, a larger focus is placed on the monitoring approaches, particularly those germane to corrosion. For SAWSs, monitoring corrosion requires an acknowledgement of the molecular and physical processes responsible for metal degradation. Using information on WWII aircraft construction, insights from corrosion studies, and examples of applied corrosion theory, the current understanding of how corrosion impacts SAWSs is summarized. It is from this synopsis that the glaring void regarding the role of microorganisms is revealed. The causes of MIC, especially those relevant to submerged aluminum, are covered prior to a concise literature review on MIC studies in UCH contexts. While none have focused on SAWSs, the diversity of approaches and research questions offers both a foundational understanding for the current project's intentions and an idea of where future examinations of MIC could go. With sufficient background on SAWSs, in situ preservation, and MIC provided, the current study sites are discussed, including the historical context, physical descriptions, and previous archaeological investigations. Chapter 1 concludes with the overall project objectives, hypotheses, and expected significance.

Chapters Two, Three, and Four are written as articles for publication in peer-reviewed journals. As such, the content of each chapter is tailored towards the journal's goals and intended audience. This decision was made in an effort to increase the research's dissemination through journal readership, while enabling a critical evaluation of each chapter through the peer review process. The lengthier Introduction and Conclusion chapters are a way of fully contextualizing ideas touched upon in the intervening chapters, making explicit the connection between the three articles and relating the content espoused in them back to the overall goal of contributing to SAWS management. Thus, there may be some redundancy, as information covered in the opening and closing sections of this dissertation, is repeated in Chapters Two-Four for the benefit of publication and journal readers.

Chapter 2 was published in the Fall 2021 edition of *Conservation and Management of Archaeological Sites*. The article focuses on the recently revived US Navy Trade and Exchange Program (NTEP). Through this Department of the Navy (DON) initiative, certain legal avenues that enable authorized salvaging of SAWSs are opened. Beyond defining the legislative underpinnings of the NTEP, Chapter 2 traces the ethically-dubious history of SAWS recovery in an attempt to anticipate potential pitfalls of renewed interest in salvage operations. In situ preservation is presented as an alternative to recovery, though justifications for this management strategy are needed. Specifically, proponents of the NTEP, routinely charge archaeologists and site managers with neglecting SAWSs and allowing unchecked degradation. Thus, scientifically-informed decisions are not only needed for the actual management of a site, but also required to counter salvor claims that in situ preservation equates to significant site loss. The chapter concludes with a discussion conceding that SAWS recovery may be advisable under select, specific conditions. However, more often in situ preservation represents a viable method of management that is potentially more beneficial for site stakeholders. The charges of inactivity levied by the warbirder community and the value of SAWS in situ preservation are used to justify the need for a comprehensive understanding of the corrosive forces that affect this site category. As underscored throughout Chapter 1 and alluded to in Chapter 2, this picture is left incomplete without proper consideration of microbial impacts.

Chapter 3 was submitted to *Advances in Archaeological Practices* in December 2023 and is currently undergoing the peer review process. The journal's emphasis on methods and emerging research trends in archaeology served as the ideal landing spot for an article detailing the current dissertation's methodology. The primary focus of the chapter is the collection protocol developed for obtaining microbial biofilm samples from four SAWSs off Maui and O'ahu. Collection via a sterilized plastic syringe following the dislodgment of biofilm material with a polypropylene spatula proved to be the most effective method. The methodological description is prefaced by summarizing the relevance of MIC and biofilms to UCH, specifically SAWSs. This overview is intended to provide readers with context for why a microbiological approach to understanding biofilms has the potential to yield valuable information regarding site management and preservation threats. The actual sampling procedures were devised following consultation with others working on marine biofilm research, as well as previously published studies. Sample collection efforts needed to obtain adequate amounts of biofilm from wreck surfaces, both corroded and non-corroded, without inflicting harm to the wreck itself. All samples, which included sediment and seawater in addition to the biofilm, had to be transported from Hawai'i to laboratory facilities in North Carolina. The geographical separation between collection and processing sites increased the risk of sample degradation. Thus, it was initially unclear if the proposed sampling methodology would generate sufficient genetic material for DNA sequencing. The near-perfect rates of DNA extraction and sequencing appear to support the collection method's efficacy. In addition to detailing these results, the chapter includes remarks on observed differences between various collection implements and DNA extraction kits, as well as the possibility of future collaborations that make use of the reproducible and affordable collection methods.

Chapter 4 is slated for submission to a marine research journal following the defense of this dissertation. In this chapter, the taxonomic data generated from the DNA sequencing referenced in Chapter 3 is presented. The expected results were informed by past studies on submerged aluminum, which suggested some level of commonality shared between biofilm communities formed on this substrate type. However, these previous efforts revealed that the environment, through the local effects of species sorting, is likely a stronger influence on microbial composition. Additionally, there was speculation that biofilm samples from corroded wreck surfaces would produce taxonomic correlations indicative of either an active role in the corrosion process or preferential attachment to visible aluminum corrosion products. The entire dataset, which consisted of biofilm, sediment, and seawater sequencing results, were subjected to multivariate analysis (i.e. non-metric multidimensional scaling [NMDS]) and more traditional ecological statistical assessments (e.g. species diversity, taxonomic evenness, and relative abundance). The aluminum biofilm samples demonstrated two distinct groupings. The first, which is expressed as Dimension 1 on the NMDS plot, consisted of sites from different islands. This included the biofilm samples from an F6F Hellcat site off Maui sharing taxonomic similarities with samples from the FG-1A Corsair site off Oʻahu, while the biofilm samples from the SB2C-1C Helldiver site off Maui were more comparable to those from the P47 Thunderbolt site off Oʻahu. Along Dimension 2, the sites plotted more in line with expectations, as the Maui and Oʻahu sites could be clearly differentiated. Taxonomically, bacteria identified as belonging to the Alphaproteobacteria and Planctomycetacia were the most abundant regardless of site. Inter-site differences responsible for the groupings along Dimension 1 appeared to be mostly driven by microbes associated with sedimentary contexts. While initially unexpected, this result was attributed to the intermittent burial of the smaller Hellcat and Corsair sites. All four sites were unanimous is failing to yield associations between corroded wreck surfaces and specific taxa. There were, however, findings that hint at the possibility that MIC may occur at SAWSs, namely the co-occurrence of anaerobic and aerobic microbes as well as the presence of sulfate-reducing bacteria capable of producing corrosive metabolites. The chapter concludes with recommendations regarding additional research that is needed for a more conclusive MIC diagnosis.

Chapter 5 aims to make explicit the relevance of the data presented in the previous chapter to the archaeological management of SAWSs. The chapter begins by identifying successes of the current study, including the development of reproducible collection methodology and production of taxonomic results that provide insights into SAWS microbiomes. The data also serves as a baseline for future comparisons, which may help elucidate information on the effects climate change (e.g. warmer sea surface temperatures, increased ocean acidification, and more frequent extreme weather events) and local water contaminants have on biofilm communities. The transition is then made to discussing the future directions of this research, beginning with an acknowledgement that interpretations of MIC's relevancy to SAWSs are currently inconclusive. An iterative approach is needed to resolve this ambiguity, where the methods used here are built upon and improved. This should include the incorporation of metagenomic studies of gene functionality, on-site coupon testing, laboratory-based mesocosm experiments, and analyses of corrosion products. Additional lines of evidence are also needed, such as the measurement of a site's electrochemical parameters and photogrammetric documentation to empirically assess site degradation. Possible forms of mitigation are also provided, representing the ideal end goal of this research. The conclusion of this dissertation consists of a synopsis of the current understanding of MIC and SAWSs, both in terms of what can and cannot be inferred. The value of this research for cultural resource managers is also reiterated, with an emphasis on the identification of next steps. Finally, the culmination of six years of research pertaining to SAWSs results in speculation on the biggest preservation threat that SAWSs currently face.

Submerged Aircraft Wreck Sites of World War II

World War II marks a defining period in our contemporary past (Moshenka 2006). This is due, in part, to its sheer scale in terms of the human life lost resulting from the rapid rise in warfare related technologies. Perhaps nowhere is this more obvious or emblematic than in the field of aviation. During World War I, which occurred just over a decade after the Wright Brothers' first successful flight, airplanes played a relatively minor part when compared to trench warfare and the actions of ground troops. This changed tremendously during WWII, as aircraft assumed a much more prominent role. This ranged from the famed dogfights occurring in the skies of both theatres to the bombing strategies employed by the Allied and Axis powers. Aircraft production reached prolific heights, with nearly 300,000 planes manufactured in the US alone (Office of Statistical Control [OSC] 1945:112). The newfound reliance on flying spurred the development of airpower doctrines, which forever changed the perception of aircraft and how war is conducted (Call 2009; Crane 1993; Deptula 2001; Quester 1978; Raines 2000).

Today, examples of WWII aircraft can readily be seen around the world in the form of crash sites, serving as a poignant reminder of the war's destructive reality. The US Army Air Forces (USAAF) are reported to have lost 65,164 aircraft during the war (OCS 1945:184), while estimates for the United States Navy (USN) are as high as 30,000 planes (Chapter 2). The aerial carnage is a combined result of combat and accidents, indicative of the risks inherent to aviation warfare. On land, decades of salvaging and recovery has drastically reduced the number of in situ wrecks (Fix 2011). Thus, the world's bodies of water represent the largest reservoir of genuine WWII aircraft (Gillespie 2011). According to the Naval History and Heritage Command's (NHHC) Underwater Archaeology Branch (UAB), who is tasked with managing the USN's submerged cultural resources, over 15,000 USN SAWSs are believed to exist.[2] This total may be an underestimation of USN aircraft sites in aquatic contexts, as planes were intentionally dumped into the ocean at the end of the war during operations intended to facilitate the return of servicemembers and prevent excessive surplus (Chiles 1995). A similar database for USAAF planes does not exist, as the US Air Force (USAF) abandoned title to all pre-1961 aircraft following a records room fire (USAF 1994:104).

Submerged Aircraft Wreck Sites in Hawai‘i

The global distribution of SAWSs is owed to the vast geographical scale on which WWII was waged. This not only encompasses operational missions flown against enemy combatants, but extends to the vital and often hazardous training efforts that occurred both domestically and beyond the home front. Within the US, this has resulted in a proliferation of SAWSs in stateside waters, including the Great Lakes, Gulf of Mexico, and the Hawaiian Islands. The last of these three constituted the center of strategic operations in the Pacific, earning the nickname ‘Crossroads of the Pacific’ as it was a transit point for nearly every aviator and aircraft that saw action in the Pacific Theatre (Horvat 1966; Pearl Harbor Aviation Museum 2023; Shettle 2001). Perhaps best remembered as the location of the Japanese military's attack on Pearl Harbor and the Battle of Midway, Hawai‘i also served as an invaluable training center for aircrews

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[2] https://www.history.navy.mil/research/underwater-archaeology.html

participating in the Allied forces island-hopping campaign. The volcanic archipelago offered the US air forces a tropical backdrop, reminiscent of the environments that would be encountered further west. With comparable flying conditions, a vast, open ocean, and viable offshore targets, Hawaiʻi enabled aviators to hone a variety of skills that would be applicable along the frontlines. Bases on the islands of Oʻahu and Maui supported the bulk of air operations in Hawaiʻi, with the two Naval Air Stations on Maui, alone, hosting an estimated 20,000 pilots during the war (Pearl Harbor Aviation Museum 2023).

Between 1924-1952, archival records indicate that a total of 1,484 aircraft were lost in the vicinity of Hawaiʻi (National Oceanic and Atmospheric Administration [NOAA] 2011). According to the state's Inventory List of Submerged Cultural Resources (ILSCR), at least 1,375 are either known or believed to have been wrecked in the ocean, with the vast majority (95.7%) dating to the period between 1939-1949 (NOAA 2017:12). The ILSCR rates the locational data for each site on a four-point scale (confirmed, good, fair, poor). Of the SAWSs that can be attributed to the WWII-era, 41 have either good or confirmed locational data within the 'Main Eight' Hawaiian Islands (Hawaiʻi, Maui, Lanai, Molokai, Kahoolawe, Lanai, Oʻahu, Kauai, and Niihau). While 41 may appear small in comparison to the total number of aircraft lost in Hawaiian waters, it represents 19% of all historic (i.e. predates 1950) submerged cultural resources with good/confirmed locational data (Figure 1.1). Furthermore, the number of aircraft sites is likely to increase as sites are located and reported by both heritage professionals and local community members. Thus, while ships are most often conceived of as the archetypal site for underwater archaeology, aircraft constitute a sizeable proportion of the sites that fall under the purview of UCH managers in Hawaiʻi.

Cultural Significance of Submerged Aircraft Wreck Sites

The remains of sunken WWII aircraft in Hawaiʻi are not only numerous, but also imbued with a cultural significance that is both multi-faceted and legally-codified. Interest in WWII aircraft crash sites and the related physical materials, beyond the recovery of human remains, began in earnest during the 1960s with hobbyists, enthusiasts, and other special interest groups that emphasized salvaging and reconstruction (Fix 2011). Due to the ephemerality of the airscapes in which WWII planes operated, airpower has largely been "memorialized by the machines themselves" (Kohn 1995:1052). The aircraft becomes a tangible point of access where site users can reflect on the nature of the conflict responsible for the plane's existence, thus evoking feelings of patriotism, nostalgia, and remembrance (Fix 2011:992).

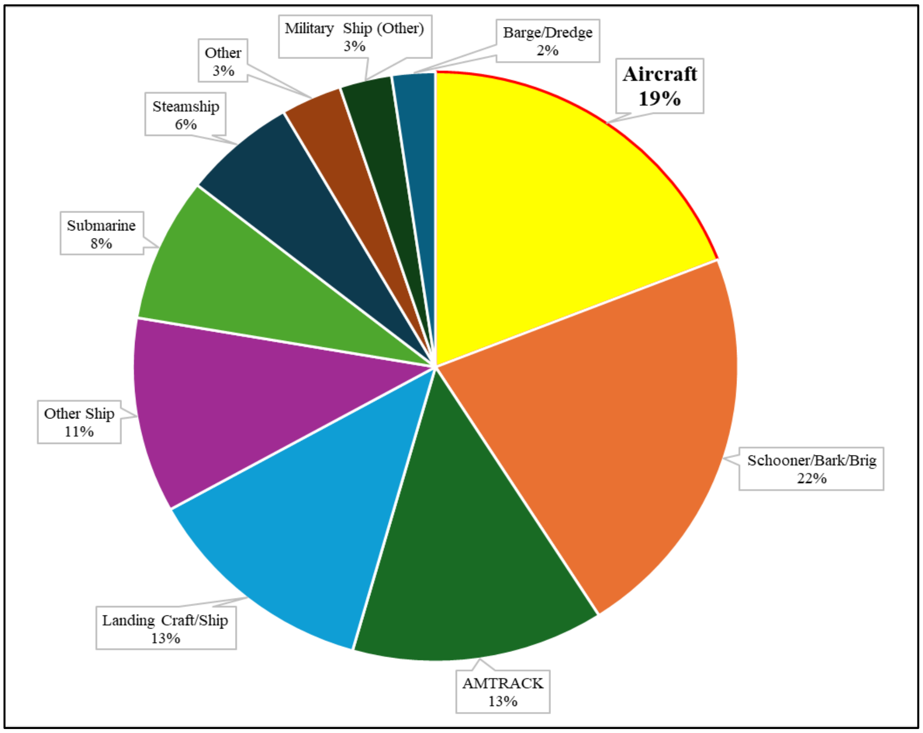

Figure 1.1. Sunken historic (pre-1950) vessels (n=215) in the Main Eight Hawaiian Island with 'Good/Confirmed' locational data according to the Inventory List of Submerged Cultural Resources (NOAA 2017).

In Hawaiʻi, the roar of aircraft traversing the skies left a considerable impression on many residents, particularly the youth. It was reportedly not uncommon for kids in Hawaiʻi to act out imaginary aerial skirmishes, or gaze in amazement at the real aircraft above their heads (Duensing 1992). The pilots themselves garnered role model status, inspiring many Hawaiian youth to volunteer with the Office of Civilian Defense, acting as stretcher-bearers, nurses aids, messengers, and community observers (Duensing 1992). Yet, the aircraft also came to symbolize the difficulties of war, including Japanese internment, military requisition of private lands, the institution of marital law, and the threat of invasion. Thus, Hawaiʻi's WWII history is defined by this complicated narrative that juxtaposes feelings of pride, victory, and a broad acceptance of WWII as a "good war" (Schuman and Rieger 1992:316), with accounts of destruction and disruption (Allen 2021; Bailey and Farber 1992; Maui Historical Society 1992; Nebolon 2017; Soga 2007; Sterner 2007; Tyler 2017; White and Lindstrom 1989). As physical manifestations of this ambivalence, WWII aircraft are subject to a continuum of individualized interpretations.

The pilfering of terrestrial crash sites, combined with the advent of self-contained underwater breathing apparatus (SCUBA) diving, fostered an increased appreciation for the aircraft wrecks that remained preserved within the ocean. In 1969, only 24 years after the War in the Pacific officially ceased, famed explorer and filmmaker Jacques Cousteau, led an expedition to Chuuk (Federated States of Micronesia) to document the 'Ghost Fleet of Chuuk Lagoon' (Bailey 2000). The Japanese 'ghost fleet' features numerous sunken planes, alongside ships and amphibious vehicles. The striking contrast of viewing machines once intended for flight, now coral-encrusted and frozen in time, offered a visceral reminder of the war's violence. Since then, WWII SAWSs have become a significant component of wreck diving throughout the world (Dimmock and Musa 2013; Edney and Boyd 2020; Jeffery 2007; McKinnon 2015), including Hawaiʻi. The desire to access these sites is tied to the same motivations that spur visitation to other wartime vestiges, including personal connections, historical interests, and morbid curiosity

(Dunkley et al. 2011; Gibson et al. 2022; Ryan 2007; Thomas et al. 2016; Yuill 2004). As expressions of WWII's "chaotic material reality," the aircraft sites provide a linkage to the past that far exceeds symbolic and textual representations of the war (González-Ruibal 2008:260). This sentiment is made especially personal when a site is correlated with a loss, which is by no means limited to combat wrecks. Domestically, over 52,000 aviation training accidents were recorded between 1941-1945, resulting in 13,873 wrecked planes (OCS 1945:309). Of the total accidents, 6,039 were considered fatal corresponding to the death of nearly 15,000 servicemembers. Thus, even before deployment to the frontlines, aircrews faced significant dangers that are now encapsulated in the SAWSs left behind. The often mangled remains invite visitors to mentally-recreate or speculate on the cause of the plane's deposition in the archaeological record. The aircraft can then be considered within relation to, both, the geographical realties present at the time of the crash, as well as the subsequent changes associated with a return to normal life during peacetime.

While the historical authenticity of WWII SAWSs continues to be an important motivator of site visitation for the reasons described, Edney and Boyd (2021:100) have argued that SAWSs may entice wreck divers through aspects unrelated to a plane's wartime role. As opposed to larger shipwrecks, the smaller-sized aircraft can be viewed on a more "human scale," thus, providing an intimate user experience. The aesthetics of SAWSs, specifically their ability to act as "fish aggregation devices," can also attract those who are more interested in the opportunity to view the diverse marine biota that colonize wreck sites (Edney and Spennemann 2015:151). Additionally, experiential motivations related to the promise of isolation beneath the surface and the perceived challenge of wreck diving amongst the recreational diving community constitute other desirable qualities of SAWSs (Edney 2017).

Management Entities for Submerged Aircraft Wreck Sites in Hawaiʻi

Though cultural significance may dictate that a wreck should be protected, it is ultimately up to the entrusted agencies with enforcement of the laws pertaining to historic preservation. The legislation applicable to the protection of SAWSs, namely the National Historic Preservation Act (NHPA) (1966) and the Sunken Military Craft Act (SMCA) (2004), are largely the focus of this dissertation's second chapter. Therefore, the following section is instead devoted to discussing the two management agencies most germane to SAWSs in Hawaiʻi. Knowing who is responsible for site management is essential to understanding the practical relevance of this dissertation. At the state level, SAWS management largely falls to the State Historic Preservation Division (SHPD)'s Archaeology Branch, which assists in the stewardship of Hawaiʻi's historic resources mainly through project review and compliance measures related to NHPA regulations and local legislation (e.g. Hawaiʻi Revised Statutes 6E).[3] The branch also maintains a vetted list of cultural resource management firms and assists with nominations to both the Hawaiʻi and National Registers of Historic Places. Unlike certain states, Hawaiʻi does not have a separate underwater archaeology office, and therefore, the SHPD's Archaeology Branch is also tasked with the management of historic resources found within state submerged lands. For Hawaiʻi, this extends from the mean higher high waterline (average level of the highest tide for each day computed over a 19-year period) to three nautical miles (nmi) offshore (Office of Coast Survey n.d.). Of the 2,120 vessel (ship and aircraft) losses mentioned in the ILSCR, at least 720 are believed to be within these state waters. The remaining 1,400 sites are listed as being within federal waters (outer continental shelf, 3-200 nmi), thus, falling under federal jurisdiction.

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[3] https://dlnr.Hawaiʻi.gov/shpd/about/branches/archaeology/

The second relevant agency is the National Oceanic and Atmospheric Administration's (NOAA) Office of National Marine Sanctuaries (OMNS). In 1972, Congress passed the Marine Protection, Research, and Sanctuaries Act (16 USC §§ 1431 et seq 1972), in response to environmental disasters that impacted marine ecosystems. Title III of the act created the National Marine Sanctuary (NMS) system that would be administered by the then-recently established NOAA within the Department of Commerce. Sanctuary designations, and the related agency responsibilities codified by the founding act, superseded state submerged land boundaries. For Hawaiʻi, the passage of The Hawaiian Islands National Marine Sanctuary and Protection Act (US Public Law 102-587), which followed on the heels of the reauthorization (1992) of the original Sanctuaries Act (1972), resulted in the establishment of 3,600 kilometers^2 (km) of waters around the Main Eight as a whale habitat sanctuary. This designation would also result in the ONMS, which was elevated from a NOAA division in 2006, being charged with coordinating efforts to "support, promote, and coordinate research on, and the conservation, curation, and public display of, the cultural, archeological, and historical resources" (16 USC §§ 1440(a) 1972). Legal responsibilities over historic resources were also conferred to the ONMS, superseding the state's ownership of wrecks per the Abandon Shipwrecks Act (1988).

The research and monitoring mandate was listed alongside calls "to enhance public awareness, understanding, appreciation, and wise and sustainable use…[of] the natural, historical, cultural, and archeological resources" (16 USC §§ 1440(b) 1972). To better facilitate this objective, the ONMS established its Maritime Heritage Program (MHP), which was created for the explicit purpose of promoting awareness regarding the sanctuaries' maritime heritage resources on a national level.[4]The MHP also represents NOAA's effort to adhere to the Federal

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[4] https://sanctuaries.noaa.gov/maritime/

Archaeological Program, and specifically the NHPA's Section 110 mandate This clause pertains to federal land-managing agencies and the expectation that they "actively search for archaeological resources and to assess them for their significance and eligibility for inclusion in the National Register of Historic Places."[5] Through this more proactive approach to heritage management, the ONMS can move away from compliance-focused objectives of site impact assessment and mitigation to more research and outreach centered activities. For Hawai'i, NOAA-backed projects under the auspices of the MHP have resulted in a multitude of archaeological surveys of UCH sites within the Hawaiian Islands Humpback Whale National Marine Sanctuary (NOAA 2017). Often a collaborative endeavor with the University of Hawai'i, these investigations have provided a font of information regarding site discovery and documentation that otherwise would have gone unrecorded. Findings have been communicated to the public through a variety of channels, including presentations, news interviews, digital displays, and partnerships with museums and educational institutions. The MHP is also credited with the creation of the ILSCR, which serves as an invaluable catalog of UCH sites in Hawai'i.

It is worth noting that the legal management of WWII SAWSs is not as straightforward as adhering to state and federal boundaries. The SMCA is not trumped by NMS designations, in the same way that responsibility of shipwrecks (non-military) in sanctuary waters passes from the state to the ONMS. Rather, the SAWSs remain property of the designated military branch and are subjected to the stipulations put forth by the SMCA. For USN aircraft, any activity that is deemed potentially disturbing to SAWSs requires permitting through the NHHC's UAB. Special Use Permits are applicable to an array of actions, ranging from scientific research to commercial salvaging and seafloor construction. In 2015, however, the DON and NOAA signed an

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[5] https://sanctuaries.noaa.gov/maritime/

Interagency Agreement regarding cooperation under the SMCA.[6] In this agreement, the DON stated that certain prohibitions listed in the SMCA were no longer applicable to either actions approved by NOAA within a sanctuary or NOAA-directed actions pertaining to sunken military craft outside sanctuary limits. Furthermore, the DON named NOAA as the "lead permitting authority for activities directed at sunken military craft…located in national marine sanctuaries."[7] In return, NOAA representatives are expected to consult with the DON on issuing any NOAA permits or other undertakings by NOAA that "may disturb, injure, or remove a sunken military craft."[8] For USAAF aircraft, the abandonment of title and interest by the military has resulted in the Secretary of the Air Force transferring responsibility to the land manager (USAF 2021:184). In these instances, determination of the relevant management agency reverts back to the distinction between NMS waters and state submerged lands, with NHPA and local historic preservation laws likely applicable.

Submerged Aircraft Wreck Sites Management and Uses

The scarcity of resources (e.g. budget, personnel, time), the richness of UCH, and concerns about the impacts of the natural environment on site preservation forces both the SHPD and ONMS in Hawai'i to confront significant questions regarding the appropriate site management strategy. For SAWSs, this decision often boils down to a choice between in situ preservation and recovery. For the purposes of this project, in situ preservation is defined as:

> "[A]ny steps taken on a site or intervention with a site in order to extend its longevity while maintaining original context and spatial position; while artefacts and features may have been excavated and/or removed, the site itself remains in place and retains all or a majority of its original context," Ortmann et al. (2010:28).

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[6] Interagency Agreement between the National Oceanic and Atmospheric Administration of the United States Department of Commerce and the United States Department of Navy on Cooperation under the Sunken Military Craft Act. Dated 10 June 2015.

[7] See Interagency Agreement.

[8] See Interagency Agreement.

This definition makes clear that in situ preservation is not an ‘all-or-nothing’ endeavor, meaning that the only two outcomes are total loss or perfect preservation. Rather, the desired outcome is often between these two extremes, where site managers seek to conserve the majority of a site, while accepting some inevitable decay (Bulut and Yüceer 2023; Gregory et al. 2012; Manders 2008; Richards and McKinnon 2009; Ortmann et al. 2010; Ricca and La Russa 2020). Yet, those who wish to see the recovery of SAWSs have tended to equate in situ preservation with inactivity and presumed site loss, as chronicled in Chapter 2. Such conceptualizations of in situ preservation ignore the true spectrum of methods and responses that this form of site management entails. Furthermore, proponents of SAWS recovery often minimize the unsavory consequences of dismantling sites and consigning aircraft to private collections, which does little to benefit the majority of stakeholders.

At a disciplinary level, the preference for in situ preservation has been codified by the Annex to the 2001 UNESCO *Convention on the Protection of the Underwater Cultural* Heritage, which serves as the guiding set of principles for underwater archaeologists (UNESCO 2001b). The Annex lists in situ preservation as the “first option,” though retrieving either parts or the entire wreck can be done if “authorized in a manner consistent with the protection of that heritage” (Rule 1, *Annex: Rules Concerning Activities Directed at Underwater Cultural Heritage*). The Convention, itself, goes on to defines what can be considered as UCH, the societal implications of UCH, and the outline of an international, cooperative framework for protecting the world’s UCH resources. While the US has yet to formally ratify the convention due to jurisdictional concerns (Varmer et al. 2010), numerous US management agencies, including but not limited to the Department of Defense, NHHC, NPS, NOAA, Bureau of Ocean

Energy Management, and the Advisory Council on Historic Preservation have adopted or support the Annex in its entirety as Best Management Practices.

Yet, there remains important questions surrounding the privileging of in situ preservation. Ortmann (2009) correctly highlighted that cultural resource managers should understand the benefits of in situ preservation, which entail more than simply regurgitating phrases such as ‘public access’ or the ‘benefit of future generations.’ Instead, site managers should explicitly conceptualize in situ preservation as a ‘public good,’ available for not only future stakeholders, but current ones, as well. This is especially true when a large portion of UCH in situ preservation projects are supported by public funds. Thus, the movement within historic preservation towards the in situ ethos was largely borne out of this desire to maximize both service to the public and agency resources (Gregory 2009; Maarleveld et al. 2013; Manders 2008; Ortmann et al. 2010; Scott-Ireton 2020). In situ preservation is often viewed as a sensible way to protect a submerged site after initial discovery that avoids the logistical concerns of full-scale or partial recovery, while buying additional time to consider management alternatives. The financial burdens of recovery were made evident by the European Civil Aviation Conference (ECAC 2012:15), which provided the following formula that can be used to explain how SAWS recovery costs can reach insurmountable heights:

> $total_{cost} = m_{cost} + (rt) + d_{cost} + c,$ where m_{cost} are mobilization costs (hiring of specialist personnel and equipment), rt is the product of the daily rate and duration of the project, d_{cost} are demobilization costs, and c are consumables (estimated to be an additional 20% of the overall budget)

Koerner (1999) estimated that salvaging projects focused on historical marine resources routinely surpass $30,000 per day, which can far exceed the costs associated with in situ preservation efforts. Recently, a project that recovered a 1940 Curtiss SB2C-4E Helldiver from off the coast of Martha's Vineyard ended up costing the Army Corps of Engineers two million dollars for the recovery alone (Asimow 2019). In the Netherlands, an ambitious project to recover some 30 WWII-era planes from both terrestrial and aquatic locales was estimated to cost around fifteen million euros (Pieters 2018). Price tags such as these can be sufficient justification for opting to preserve UCH in situ as opposed to recovery. Yet, the removal of a wreck from its watery resting place is only the beginning, as recovery projects must be accompanied with plans for conservation and storage. This creates additional financial burdens related to facilities, the hiring of conservation experts, and potentially expensive laboratory procedures necessary for housing a previously submerged object on land.

Non-Consumptive Uses of Submerged Aircraft Wreck Sites

Beyond the financial justification of opting for in situ preservation over recovery, leaving SAWSs in place, presumably in a publicly accessible area, enables site visitation. Wreck diving both in Hawai'i and worldwide attests to the fact that recovery and placement in a museum is not the only way of ensuring site access. In situ site visitation can be considered a 'nonconsumptive use' (Finney 2002; Kaoru and Hogland 1994; Stolk et al. 2007), which is a stark contrast to the salvaging and looting of historical aircraft that defined the early years of aviation archaeology (Fix 2011). Even those who do not physically interact with a wreck site may wish to see its continued preservation due to the aforementioned cultural significance of WWII aircraft, especially as it relates to issues of national identity. This can be linked to a number of nonmarket values, which include the desire to simply know a site still exists (existence value), knowing one has the option to visit a site (option value), and the hope that the site will be around for use by future generations (bequest value) (Kaoru and Hogland 1994). RMS *Titanic* is perhaps the ultimate example of how nonmarket values are used to justify the expenditure of significant resources on the in situ preservation of a site that will never be visited by the vast majority of interested stakeholders (Gongaware 2011; Varmer and Aznar 2012; Varner 2012). Though non-market values are notoriously difficult to quantify in dollar amounts (Flores 2017; Milne 1991), their consideration helps to combat salvor justifications that emphasize potential revenue.

Site access can be complimented by efforts to increase users' ability to interpret sites, as exemplified by the establishment of maritime heritage trails that operate as de facto underwater museums (Leshikar-Denton and Scott-Ireton 2007; Philippou and Staniforth 2003; McKinnon 2013; Scott-Ireton and McKinnon 2015; Smith 2007). Rather than conceptualizing each wreck as an isolated site, heritage trails are intended to contextualize resources within relation to both one another and the broader seascape (McKinnon 2013, 2023; McKinnon et al. 2014). Archival research, consultation with local community members, and archaeological investigations can be synthesized into educational materials, both digital and physical (e.g. dive guides) that convey relevant historical background information on each site (McKinnon and Carrell 2018; Price 2013; Scott-Ireton 2015). Trail access is often free and available to dive companies, which hints at the economic potential for successful UCH management (McKinnon 2015).

Heritage Tourism

The promotion of SAWSs for nonconsumptive uses related to recreational diving helps to diversify and, potentially, increase economic opportunities within the tourism sector. In Hawai‘i, tourism is the unquestionable economic driver, despite a near-total disruption in 2020 during the COVID-19 pandemic (Department of Business, Economic Development and Tourism [DBEDT] 2023a). Tourism's contribution to the Hawai‘i gross domestic product (GDP) was estimated to be almost 18% if only direct and indirect impacts are included (DBEDT 2023b). This total could be as high as 24% if all impacts (direct, indirect, induced) are considered, with 20-25% of all jobs in

Hawaiʻi falling within the tourism sector. When the contribution of tourism to other sectors is accounted for, tourism is the highest contributor to the state's GDP, followed by the real estate market (15%) (DBEDT 2023b). Using the latest available data from the 2022 fiscal year, Hawaiʻi received 9,233,983 visitors, which equated to around $19.8 billion in total expenditures and a daily average of $232 per visitor (DBEDT 2022). The arrivals count represents about a 90% recovery from pre-pandemic levels, despite the Japanese visitor market only reaching about 32% of its pre-pandemic level (Hawaiʻi Tourism Authority [HTA] 2023). While the expenditures were the highest ever (not adjusted for inflation), both total and daily spending is expected to grow +4.3% and +4.5%, respectively, by next year (HTA 2023).

This economic reliance on tourism in Hawaiʻi has been met with significant controversy and criticism (Assante et al. 2012; McDonagh 2022; Pallett-Wiesel 2022; Pollitt 2020; Woo 2009), examples of which can also be found for many island locales that depend on traditional SSS (sun, sea, sand) tourism (Alberts and Baldacchino 2017; Bojanic and Lo 2016; Cameron and Gatewood 2008; Harrison and Pratt 2015; Hezel 2012; Kelman 2019; Pratt 2015; Roudi et al. 2019; Timothy 2022). Thus, sustainability through various forms of eco-tourism was originally hailed as an 'economic panacea' for tropical islands, as it is intended to minimize the need for destructive construction developments (e.g. resorts, shopping centers, parking lots) (Blamey 1997, 2001; Buckley 1994; Fennell and Eagles 1990; Lieberknecht et al. 1998; Ruschmann 1992; Spennemann et al. 2001). While the merits of this sentiment have since been debated (Das and Chatterjee 2015; Fletch and Neves 2012; Ghosh and Ghosh 2019; Krüger 2005), proponents of eco-tourism continue to highlight the use of existing natural and cultural resources as the main attractions (Barna et al. 2011; Boley and Green 2016; Hunt et al. 2015; Mensah 2017; Moli 2011; Oladeji and Kayode 2013; Rosenfeld 2008; Salman et al. 2020; Stronza et al. 2019).

Research on the management of UCH has consistently revealed that, when undertaken correctly, underwater archaeological sites can act as a profitable, yet sustainable, earner for the host communities (Firth 2015; Jeffery 2004). Such practices are used in the promotion of heritage tourism, which is among the fastest growing forms of eco-tourism (Hall 2016). The National Trust for Historic Preservation has defined heritage tourism as "traveling to experience the places, artifacts, and activities that authentically represent the stories and people of the past and present."[9] General motivations for engaging in heritage tourism are similar to those associated with SAWS visitation, including education, curiosity, nostalgia, leisure, social cohesion, and as means of finding one's cultural identity (Poria et al. 2004; Timothy & Boyd 2003; Timothy & Nyaupane 2009). At its heart, heritage tourism attempts to turn "socio-cultural assets" into an economic activity through the attraction of visitors (Chhabra et al. 2003:703). Since the 1990s, heritage tourism has grown relatively quickly compared to other forms of tourism, comprising around 35-40% of the tourism market (O'Leary et al. 1998; Hall 2016). Studies suggest that while visiting heritage sites may not be the primary motivation, nearly 80% of recreational travel involves cultural heritage experiences in some form (Timothy 2011, 2018). At least part of this growth is motivated by a postmodern desire to bond with the past, often on a personal level and in the face of an increasingly modernized, disconnected world (Garrod and Fyall 2000). Heritage tourists not only financially benefit the businesses (e.g. dive operators) directly involved in heritage-centered activities, but act as an economic multiplier through expenditures related to the hospitality sector (e.g. hotels, restaurants, car rentals) and other services (Bonet 2013; Cela et al. 2009; Strauss and Lord 2001; Timothy 2015).

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[9] https://www.nps.gov/subjects/teachingwithhistoricplaces/heritage-travel.htm

Conceptualizing UCH as a means to achieve sustainable development led to the development of the UNESCO (2017) *Safeguarding Underwater Cultural Heritage in the Pacific.* The work of various researchers to produce this report on the best practices for the protection and management of WWII UCH is intended to support the UN *2030 Agenda for Sustainable Development* and its Sustainable Development Goals (UN 2015). A similar effort was made in 2010, when UNESCO released *Underwater Cultural Heritage in Oceania* (Guérin et al. 2010). Beyond inventorying UCH sites in the Pacific, the report draws explicit attention to the ways in which UCH is economically significant in this region. Recently, the linkage between sustainable development and UCH came to light with the onset of the UN initiative *Decade of Ocean Science for Sustainable Development 2021–2030* (the Decade). Though heritage resources are not the focus, maritime archaeologists have argued convincingly that the Decade is a prime opportunity to incorporate existing UCH into broader sustainability efforts, especially through interdisciplinary collaboration (Henderson 2019; Lee 2019; Trakadas et al. 2019). Examples can include UCH management that is incorporated into marine spatial planning efforts that seek to synergize in situ preservation with other marine activities (e.g. fishing, resource extraction, offshore energy generation, and coastal development) (Argyropoulos and Stratigea 2019a; Brennan et al. 2016; Papageorgiou 2018; Secci 2011). The successful incorporation of UCH preservation into legislative and commercial agendas helps to ensure that stakeholders, both current and future, retain access to sites.

In Hawaiʻi, the potential of heritage tourism is bolstered by the archipelago's reputation as a premier destination for those seeking to engage in island and/or marine tourism. Rather than relying on the heritage tourism attractions (e.g. SAWSs) as the primary motivation, UCH can be promoted amongst a robust consumer base that is predisposed to interacting with the ocean.

While at some tourism destinations the coast competes with inland and other non-marine attractions, Hawai‘i’s touristic allure is innately maritime-focused. Amongst US tourists, visiting the beach was by far the most popular recreational activity (87%), with 69% and 45%, respectively, of survey respondents reporting that they also swam and snorkeled in the ocean (DBEDT 2023c). Yet, cultural heritage also constituted a significant attraction, as military (23%), Native Hawaiian (33%), and other historical sites (14%) were frequented by visitors (DBEDT 2023c). World War II heritage seems to be especially popular, as O‘ahu’s Pearl Harbor was visited by up to 40% of survey respondents, trailing only the famous North Shore (46%) as the island’s most popular attraction (DBEDT 2023c). The NPS estimates that around 1.5 million people annually visit the primary site of the Japanese military’s attack.[10] Though USS *Missouri* and the USS *Arizona* Memorial are perhaps the main draws, the Pearl Harbor Aviation Museum (PHAM) reported a total of 242,871 visitors and a total revenue of $12.2 million in its latest annual report (PHAM 2022). Thus, the visitor demand for ocean and WWII themed experiences in Hawai‘i is abundantly clear. While virtually no research has been conducted regarding the combination of the two, it stands to reason that, if appropriately promoted, WWII UCH sites, particularly SAWSs, could contribute significantly to the Hawaiian economy.

Though SCUBA diving was only acknowledged by ~2.5% of visitor survey respondents (DBEDT 2023c), it is often considered a high-price leisure activity associated with greater expenditures than other forms of recreation (Davis and Tisdell 1996; Dimmock and Cummins 2013; Pendleton and Rooke 2006; Saayman and Saayman 2018). Extrapolating the average percentage (2.5%) of survey respondents who participated in SCUBA diving to the total number of visitors in 2022 equates to an estimated 277,019 diving tourists. The average cost ($180) of a

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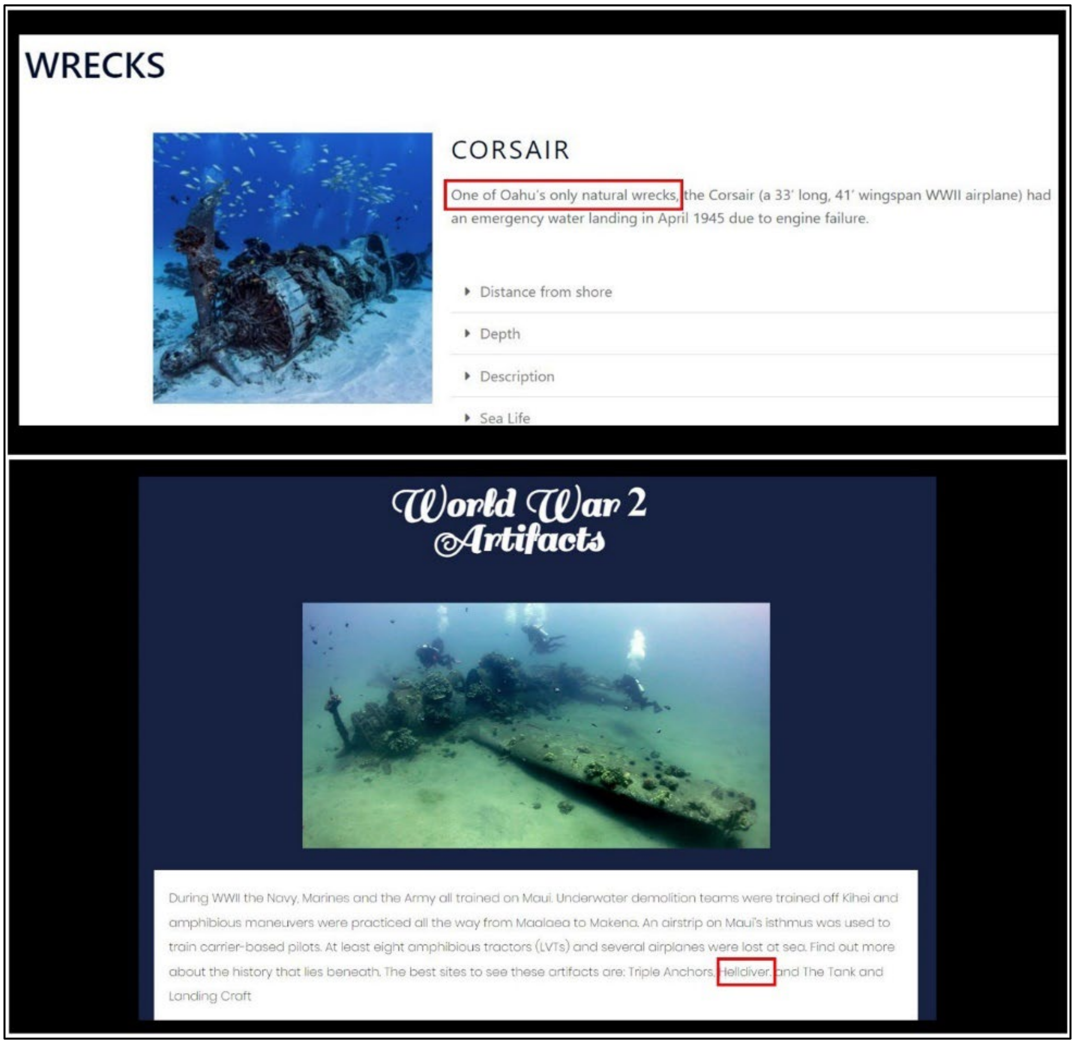
[10] “Annual Park Recreation Visits (1981 – Last Calendar Year).” https://irma.nps.gov/Stats/Reports/Park/PERL

“guided tour for certified divers” was calculated for the top-10 (Google) most reviewed SCUBA operators on Oʻahu. Thus, a hypothetical direct contribution of SCUBA diving tourism to the Hawaiian economy, not accounting for services associated with the hospitality sector, is $41.5 million dollars. For wreck diving specifically, willingness to pay studies indicate that potential economic benefits vary with issues of geography, historical importance, personal motivations, and other contextual factors. As Kaoru and Hoagland (1994:206) wrote, “Visitors are willing to incur higher travel costs by traveling farther only if their recreational benefits from nonconsumptive uses of the [wreck] resources at the destination sites are higher.” The opportunity to interact with perhaps the premiere symbol of WWII may yield sufficient ‘recreational benefits.’ This plausibility is likely responsible for two SAWSs in Hawaiʻi, a Vought F4U Corsair off southeastern Oʻahu and a Curtiss SB2C-1C Helldiver off southern Maui, being featured amongst local diver operator websites (Figure 1.2). The former aircraft is often (mistakenly) advertised as one of Oʻahu’s only “natural wrecks,” as SCUBA guides attempt to capitalize on the plane’s historical background as a marketing strategy.

Digital Presentation of Submerged Aircraft Wreck Sites

Yet, with today’s technology it is now entirely possible to present UCH sites to nondivers. The proliferation of 3D modelling programs has enabled the transformation of site photos into easily-constructed digital models that can be accessed remotely via the internet (Bruno et al. 2017; Erič et al. 2017; McCarthy et al. 2019; Yamafune 2016). Similarly, immersive virtual reality programs can even give users the experience of being on a wreck while it lays on the seafloor (Bruno et al. 2019; Čejka et al. 2020; Secci et al. 2019). Physical museums are no longer the only place one can view maritime cultural resources, and thus, recovery is no longer the only way of presenting these materials to the public. A site can remain in situ, while its digital documentation can be used for educational and entertainment purposes, much in the same way a traditional museum operates.



WRECKS

CORSAIR

One of Oahu's only natural wrecks, the Corsair (a 33' long, 41' wingspan WWII airplane) had an emergency water landing in April 1945 due to engine failure.

During WWII the Navy, Marines and the Army all trained on Maui. Underwater demolition teams were trained off Kihei and amphibious maneuvers were practiced all the way from Maalaea to Makena. An airstrip on Maui's isthmus was used to train carrier-based pilots. At least eight amphibious tractors (LVTs) and several airplanes were lost at sea. Find out more about the history that lies beneath. The best sites to see these artifacts are: Triple Anchors, Helldiver, and The Tank and Landing Craft

Figure 1.2. Online advertisements for SCUBA dive tours on the Corsair site off O'ahu and the Helldiver off Maui.[11]

From a monetization standpoint, digital documentation of UCH sites has the potential to be commodified through the creation of non-fungible tokens (NFTs). The NFT itself is not the digital object, but rather unique identifiers recorded on a ledger (blockchain) that certify authenticity and ownership (Ghelani 2022). Akin to limited edition trading cards, NFTs are

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[11] Corsair: https://www.aaronsdiveshop.com/oahu-dive-sites/; Helldiver: https://www.diveislandstyle.com/divesitesonmaui

designed to infuse a modern item with relic (collectable) value (Hales 2023). Recently, this strategy has been employed by art museums, offering patrons a chance to ‘own’ classical works (Abiuso 2021; Kulakova 2022). Prompted by pandemic-induced financial strains, Italy’s Uffizi Galleries began releasing NFTs for digitalized versions of their collection, including Michelangelo’s painting Doni Tondo (1505–06) that sold for $170,000 (Abiuso 2021; Solomon 2021). A similar framework could exist for SAWSs, transforming remote sites into a form of exportable heritage without compromising in situ access. While the debate surrounding the long-term success of NFTs continues (Bouzid et al. 2023; Levi 2021; Raman and Raj 2021), its inclusion in this discussion is meant to serve as an additional justification for the investment in SAWS in situ preservation.

In Situ Preservation

Rather than continuing to discuss in situ preservation abstractly, attention will now be paid to the methods available to UCH managers. This review is intended to demonstrate the forms of in situ preservation applicable to SAWSs, thus providing context and rationale for the microbiological undertakings associated with this dissertation. Some strategies are currently in use by site managers in Hawai‘i, while others were found to be ineffective, inappropriate, or not applicable. For SAWSs, minimal intervention would appear preferrable due to financial considerations and a longing to allow a site to remain accessible (Argyropoulos and Stratigea 2019a, 2019b; Catsambis and Morrand 2013; Gambin et al. 2021; Lickliter-Mundon and Leverenz 2023; Ortiz and Atcheson 2023). While the latter has been discussed as a way of generating economic benefits from UCH in a generally sustainable manner, decisions regarding the chosen form of in situ preservation should still keep in mind the potential detriment that site visitors, especially tourists, pose to archaeological sites. Spennemann (1992) referred to the tourist as the fourth horseman of the apocalypse for WWII sites in the Pacific.

Negative site impacts from anchoring, mooring, vandalism, artifact looting/movement, the erection of unauthorized memorials, increased exposure to oxygen from diver bubbles, and physical contact by divers are all readily observed in the Pacific (Browne 2019; Edney 2018; Grenier and Cochran 2006; Howard 1999; MacLeod et al. 2011; McKinnon, 2015). Additionally, SAWSs are prone to specific diver behaviors that are associated with their more personal scale, including the infamous cockpit photo opportunities (Edney and Boyd 2021; McKinnon 2015). While laws restricting many of these practices exist, enforcement can often be weak and ineffective due to the difficulties (e.g. lack of personnel and vessels) involved with maintaining a constant presence on the water. Thus, preserving a site as is and allowing physical site access often involves “tradeoffs inherently linked to competing, conflicting objectives,” which has been deemed the “management dilemma” (Loomis and Peterson 2014:7). In situ preservation’s method should seek to find the balance between promoting site use and ensuring the historic resource is maintained for future generations. For the anthropogenic impacts, heritage preservation legislation can be combined with educational efforts that aim to increase ‘voluntary compliance’ that reduce the frequency of undesirable actions (Edney 2016, 2018; Edney et al. 2021; Price 2013). More restrictive measures, ranging from barrier cages built around a wreck site (Scott-Ireton and McKinnon 2015; Zmaic 2009) to outright moratoriums on site access (Becatoros 2019), can be employed in situations regarding heritage deemed to be exceedingly vulnerable or important. The limiting of public experiences and potentially displeasing aesthetics, however, are antithetical to the promotion of SAWSs as heritage tourism resources available to the public. Thus, one must be explicit about the preferred outcomes when determining the best course of action.

Stabilization

The effect the natural environment has on SAWSs, including corrosion, extreme weather events, and oceanic forces (e.g. swell, currents, and sediment scouring), remains impervious to legal mandates and social contracts that agree upon the importance of historic preservation. To confront the threats outside the realm of human agency, in situ preservation methods can essentially be divided into two parts: stabilization and monitoring (Nyström Godfrey et al. 2007; Richards et al. 2009a). Here, stabilization refers to a suspension of the physico-chemical and biological impacts causing site degradation (Richards 2011). Projects that seek to rebury UCH sites following the initial discovery or exposure represent a restrictive approach, akin to the barrier cages referenced earlier. This is most often conducted in correlation with accidental discoveries, where sites are unintentionally exposed during construction projects, storm events, or other sediment disturbances. In other cases, archaeologists and site managers purposely expose a site in order to gain insights into site layout, identification, or other points of interest (Bendig and Budsberg 2016; Gregory 2020). In both scenarios, the quasi-equilibrium reached between the physical state of the site and its burial environment is disrupted. Corrosive forces that were once minimized or prohibited, are allowed to increase as a result of new chemical reactions brought on by exposure. The reburial of a site, then, is often performed out of a desire to protect the heritage resources from further, immediate alteration (Gregory 2020; Ortmann 2009; Richards 2011; Shefi and Veth 2015; Staniforth and Shefi 2010). Reburial also allows archaeologists and other researchers to study the site in greater detail at another time (Richards et al. 2012; 2016; Veth et al. 2013). Numerous methods of reburial have been employed in UCH protection, including the use of various materials (e.g. sandbags (Richards 2011b), geotextiles (Gregory and Matthiesen 2012), and artificial seagrass (Gregory et al. 2008) to collect sediment on top of a site.

While burying a site may prevent some forces of decay in the present, keeping a site buried for an indefinite period disservices a large number of current stakeholders. Reburial as an in situ preservation method should then be reserved for sites that face immediate threats of destruction or have not been properly documented (Marano 2015; Shefi and Veth 2015). In the case of SAWSs, reburial upon discovery or exposure is most appropriate when there is a chance the site is correlated with unrecovered human remains. In such instances, the objective good associated with the return of a deceased servicemember outweighs the practical utility generated from recreational site visitation. Most sites that serve as regular wreck dives were previously evaluated for an association with a loss, and thus, this possibility is most applicable to newly-located aircraft. Discovery can be both intentional, such as remote sensing or visual surveys intended to find a specific wreck thought to contain human remains, or a coincidental byproduct of activities targeting the seafloor (Abbey et al. 2023). In either case, the site can be reburied until a proper excavation project can be mounted. Within the US, such projects usually fall under the jurisdiction of the US Department of Defense POW/MIA Accounting Agency (DPAA).[12] Whether through in-house personnel or partnerships with external organizations, the DPAA uses congressionally-appropriated funds for the recovery of fallen servicemembers in foreign wars. The DPAA adheres to a mandate that prioritizes recovery of human remains over archaeological documentation, with excavation and site reburial protocols that almost assuredly result in substantial site disarticulation and precludes subsequent site visitation (DPAA 2022). While

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[12] https://www.dpaa.mil/Our-Missing/Past-Conflicts/

clearly outside the scope of the current dissertation, the mission of the DPAA can conflict significantly with the NHHC's goal of preserving the USN's historic resources. From personal experience and conversations, the interagency friction between the DPAA and NHHC may be a prominent issue regarding SAWS management moving forward.

Reburial is intended to create pre-disturbance conditions that foster a steadiness between the wreck material and the environment, and thus is considered a form of passive stabilization (Richards 2011a). Several multi-year investigations regarding the efficacy of reburial as UCH preservation tool have confirmed this strategy's ability to slow environmentally induced deterioration (Bergstrand and Nyström Godfrey 2007; Nyström Godfrey et al. 2012; Richards 2011b; Richards et al. 2012; 2016; Veth et al. 2013). Some reburial projects, however, have been accused of being reactionary, and performed without a greater consideration for the ultimate end goal (Harvey and Shefi 2014; Shefi and Veth 2015).

Thus, there are more active steps available to site managers. Ian MacLeod and his Australian colleagues have championed the use of sacrificial anodes that are intended to slow corrosion brought upon by metal being submerged. Anodes, made of a more reactive material such as zinc, are directly attached to a wreck in hopes of providing cathodic protection (MacLeod et al. 1986). This forms a corrosion cell, where the wreck metal no longer acts as the anode, and thus, halts the release of ions during the formation of corrosion products. Instead, the wreck acts as the cathode, with the attached zinc anode releasing ions associated with the transfer of electrons within a corrosion cell. This has been successful for numerous in situ preservation projects that are aimed at either preserving individual artifacts (Gregory 1999; Macleod 1986; 1996; McCarthy 1988) or the overall hull structure (Heldtberg et al., 2004; Macleod, 2010; Macleod and Steyne 2011). Additional techniques include physically moving wrecks to more suitable locations for preservation (MacLeod 2019; Raupp et al. 2009) or, removing individual wreck components for reburial (Steyne and MacLeod 2011). The latter may also have the added benefit of relieving the hull of mechanical stress. Yet regardless of the stabilization method, those entrusted with carrying out in situ preservation of UCH are unanimous in their emphasis on the need for monitoring. Gregory (2009:9) makes this point by saying a site manager's responsibility does "not stop once the site is stabilized" and that "[m]onitoring of stabilized sites is necessary to ensure continued stability." The importance of monitoring sites, including the use of biological and molecular surveys, is key in evaluating the efficacy of in situ preservation procedures and determining future courses of action.

Monitoring

The most basic and economically-feasible UCH monitoring methods are often visual inspections. These can be executed using either divers or remote-sensing equipment (e.g. Remotely Operated Vehicles), depending on the site's depth and environment. Visual surveys, especially when accompanied with a checklist and underwater photography, can be used to methodically identify recent alterations or damage to a wreck (Jeffery et al. 2007; Murdock and Stewart 1995; Roth et al. 2022). This includes detecting negative human impacts to the integrity of a wreck's overall structure and the structure of individual components, including obvious anchor strikes, missing wreck features due to looting, vandalism, and other forms of inappropriate contact. Additionally, the visual assessment can provide insights into the biological communities inhabiting a site, which highlights the artificial reef role UCH can play (Feary et al. 2011; Richards et al. 2009b). Surveys should be designed so that participants can systematically record instances of impairment to a wreck and classify these instances by the most likely cause (i.e. cultural or natural). When visual inspections are conducted at regular intervals, site managers are better able to track the physical status of a wreck, while also assessing the prevalence of certain preservation threats. These capabilities are enhanced considerably when combined with photogrammetric techniques that provide a visual record of changes to a wreck's condition (Rossi et al. 2019).

Even with advances in underwater imaging technology, microscopic threats to a site can remain undetected. Corrosion, the "deterioration of materials due to reactions with their environment" (Stansbury and Buchanan 2000:1), is chief among these hazards. While visual evidence for corrosion can take the form of pitting and oxidized-metal build up, it is impossible to conclusively determine the rate of corrosion without a more scientifically-rigorous approach. Lacking accurate information on corrosion rates, site managers will not be able discern if a wreck is experiencing accelerated corrosion, which may necessitate mitigation efforts (e.g. sacrificial anodes). To combat this issue, interdisciplinary collaborations between archaeologists and conservation scientists have led to the development of effective corrosion survey protocols.

Corrosion Surveys

Starting in the 1980s (MacLeod 1981; 1984; 1989; North and MacLeod 1987) with steady improvement since, researchers have been ascertaining the corrosive characteristics of wrecks through measurements of pH and corrosion potential (E_{corr}). This typically involves researchers scraping or drilling through concretion and other forms of biofouling to measure the E_{corr}, which is a voltage reading at the wreck's surface that is compared to a reference electrode (e.g. silver chloride). This information is used to determine the rate of electron transfer from the corroding metal (anodic site) and the cathodic site where oxygen reduction occurs (North and MacLeod 1987). The pH value can indicate the amount of hydrogen ions present, which results from hydrolysis (i.e. the chemical breakdown of compounds by water). Both E_{corr} and pH can be measured using a specific procedure and set of recording tools that are described by Macleod (2002). The information can be plotted on metal-specific Pourbaix diagrams in order to determine if an object is in a passivated or active state of corrosion (MacLeod 1989; Pourbaix 1963). Furthermore, pH and E_{corr} readings can be combined with information on concretion thickness, rugosity (surface roughness), and other site characteristics through specified equations to produce an overall corrosion rate (MacLeod and Richards 2011; MacLeod et al. 2007; 2011). Corrosion rates not only differ between sites, but they can vary within a single site. This may be due to differential corrosive properties of metal types (i.e. galvanic corrosion) in contact with one another at a wreck site. Here, the more reactive metal acts as an anode, and thus, undergoes accelerated degradation as a form of galvanic corrosion (North 1984; Richards et al. 2009b). Similar to how it may be prudent to purposely disarticulate parts of a wreck to alleviate mechanical stress, managers can consider disconnecting certain wreck features in hopes of preventing further galvanic corrosion (Winton 2015). Alternatively, intra-site corrosion rates can be affected by wreck orientation (e.g. certain wreck components disproportionately exposed to water movement) and environmental parameters (MacLeod et al. 2007; 2011). The latter mainly refers to the level of exposure to dissolved oxygen, which can be influenced by several factors, including water temperature, salinity, depth, slope of seafloor, and level of sediment burial.

When corrosion surveys are performed as longitudinal studies, researchers can identify and track changes in a wreck's microenvironment. The degradation data obtained during corrosion surveys, combined with visual and photogrammetric documentation, can inform site managers on when action is needed and what type of mitigation efforts are appropriate (Richards 2012). In some situations, recovery, of either the entire wreck or specific components, may be necessary given the decay trajectory. In other cases, the corrosion data can imply that a site is currently in a stabilized state, and that in situ preservation approaches are adequate, including inaction, reburial, sacrificial anode use, or physical manipulation (e.g. relocation and disarticulation). Russell and Murphy (2010) provide an excellent example of how interdisciplinary studies that aim to monitor the electrochemical characteristics of a site, in addition to assessments of a wreck's physical environment and stress loads, can lead to informative, predictive models. In this specific case, the authors reviewed the multiyear project that ultimately led to the formation of a finite element model for USS *Arizona*. This research, like other scholarly ventures designed to model the decay of a wreck, can be viewed as an investment. Rather than being forced to engage in last-minute salvage efforts, the use of funds for in situ stabilization and monitoring purposes can protect the UCH resource, while also avoiding unnecessary changes to management strategies based on guessing or incomplete information. The desire to understand decay trajectories and better predict areas of structural weakness may not only arise from wanting to retain a wreck's identifiability for divers, but can also, stem from wanting to protect the divers themselves. When collapse is imminent or predictable, managers can impose restrictions (e.g. the prohibition of wreck penetration) that aim to avoid potentially dangerous situations (MacLeod and Richards 2011).

In his exceptional review of the current knowledge regarding corrosion processes that affect iron/steel wrecks in marine environments, Moore (2015:200) highlights a deficiency as it pertains to "nondeterministic" forces. Specifically, the author states that, "[i]n order for probabilistic models to be advantageously applied for understanding the degradation patterns of corroding shipwrecks over archaeological timescales, the nondeterministic environmental interactions upon the structural integrities of these sites need to be better understood." Here, 'environmental interactions' refer mainly to microbiologically-influenced corrosion (MIC).

Unlike the previous forms of generalized corrosion described above, MIC does not proceed in a linear, predictable manner. This is due to the complex and changing nature of microbial communities which are sensitive to changes in microenvironments. For example, Melchers and Wells (2006) observed that alterations to nutrient levels can significantly affect the microorganism composition associated with steel surfaces in marine environments. Thus, it appears that the best way to confront this issue would be systematic surveys aimed at collecting information on the microbiological threats present. Manders et al. (2008:185) suggest that "biological deterioration can" and should "be assessed and measured by taking samples from the original [wreck]." Just as longitudinal studies intended to track changes to the physical appearance and electrochemical conditions of a wreck, the same can be completed to evaluate the temporal variations of a site's microbiome. By monitoring the totality of preservation threats, site managers are in the best position possible to make informed decisions regarding additional stabilization methods, corrosion mitigation efforts, and establishing recovery timelines (if necessary).

Corrosion of Submerged Aluminum

Bell (2010) recognized that SAWSs warranted a specific site formation model, including environmental impacts, that differs from the ones formed by Muckelroy (1976) and Gibbs (2006) for shipwrecks. This sentiment was further supported by Pruitt and McKinnon (2024) who analyzed a SAWSs in Saipan, demonstrating the utility of understanding how the SFPs associated with aircraft can be used to discern key archaeological insights related to site identification and depositional event. Besides the nature of the wrecking event, the use of aluminum and its alloys as the primary construction materials is perhaps the biggest influence on SFPs unique to aircraft. While the inclusion of aluminum and its alloys in aircraft dates to World

War I, it is the development of alloy Al 2024 (formerly referred to as 24S) in the 1930s that revolutionized the aviation industry in the US (Hendershot 1948; Skrabec 2017). Advanced by additional quantities of magnesium, the aluminum-copper alloy increased design strength by 20% over its predecessor, Al 2017 (17S) (Staley 1989). Beginning with the first commercially-successful passenger plane, the Douglas DC-3, in 1935, through the majority of WWII, Al 2024 (commercially sold as duralumin) constituted the main building material for aircraft production in the US (Simcoe 2014). However, this is not to say aircraft were homogeneous in their construction. This not only differed by nation and plane type (Ouissi et al. 2019), but also by component as frames, skins, and propellers required different manufacturing techniques (e.g. extrusion, rolling, and casting) and stress resistances. Thus, slightly different variations of aluminum alloys were used in the construction of various aircraft components (MacLeod 2006b; Richards and Carpenter 2015).

Yet, the basic electrochemical properties of aluminum and its alloys remain the same. Unlike steel or other ferrous material (for an excellent review of the corrosion of iron in marine settings, see North and MacLeod 1987), a protective oxide barrier (Al_2O_3) forms around a piece of submerged aluminum, resulting in the prevention of electron exchange between the aluminum (i.e. oxidation) and oxygen reduction occurring at the metal-seawater interface (Davis 1999; Ghali 2010). The protective benefits of the aluminum oxide layer often prevent the process of generalized corrosion process germane to iron-based wrecks. However, submerged aluminum is not immune to corrosion, as deficiencies in the oxide layer can lead to accelerated (localized) corrosion in specific locations (Davis 1999; Dexter 1987; Ghali 2010; MacLeod 1983). Defects can occur: 1) by chemical attacks from chloride ions, 2) at microabrasions in the wreck's surface, or 3) inconsistencies in the formation of the aluminum oxide layer that accord with the metallic composition at a particular location (Ding et al. 2009) Additionally, the efficiency of this layer is affected by the properties of the electrolyte (i.e. seawater), including pH, salinity, temperature, and current velocity (Ezuber et al. 2008).

When localized corrosion of aluminum occurs, it is most often in the form of pitting corrosion (Davis 1999; Ghali 2010; MacLeod 1983). This occurs when microcracks (pits) on an object's surface form underneath areas where the aluminum oxide layer has either broken down or remains absent due to the aforementioned mechanisms. The resulting pit maintains an oxygen concentration that is lower than the adjacent surfaces. The bottom of the pit becomes an anodic site, with electrons being transferred to the nearby areas of higher oxygen (cathodic site). The aluminum ions then migrate outwards in the pit, where they undergo hydrolysis and form aluminum hydroxide and hydrogen ions. The hydrated aluminum hydroxide then precipitates over the pit site (gray/white pustules) and constitutes the main corrosion product associated with submerged aluminum (Richards and Carpenter 2015).

The hydrogen ions have two effects: they react with the metal to further increase corrosion and they lower pH, creating an acidic environment. Thus, increases in corrosion (i.e. the release of more aluminum ions) will be reflected by decreases in pH (i.e. the production of more H^+) (MacLeod 1983; 2006b). To maintain charge neutrality, chloride ions from seawater diffuse inwards and bond with positively charged aluminum ions to form dissolved aluminum chloride. Aluminum will continue to corrode under a certain pH (<4.5) and requires a concentration of chloride ions to be present within the pit (MacLeod 1983). Electrochemically, this is expressed as the pitting potential, which is the necessary voltage (i.e. transfer of electrons or E_{corr}) needed to maintain pit growth (Szklarska-Smialowska 1999). When this voltage is below a certain threshold, the pit passivates and growth is halted. The pits themselves range in shape, from shallow depressions to deep perforations, with varying sizes in depth and radius. The pits can occur in isolation along an object's surface, or within highly concentrated areas, depending on the factors mentioned previously (Szklarska-Smialowska 1999). The pitting compromises the structural integrity of the aluminum objects, rendering them further susceptible to collapse or other forms of disarticulation (Richards and Carpenter 2012, 2015, 2018).

In terms of timing, Aluminum corrosion in seawater can begin immediately upon submergence, starting at defects or gaps in the aluminum oxide film that forms in aqueous solutions. The absorption of chloride ions at these unprotected surface areas can initiate pitting, even at relatively low chloride concentrations (~15 parts per million) (MacLeod 1983). In addition to a critical chloride concentration, pit growth is predicated on pH levels and the diffusion of dissolved oxygen at the metal-seawater interface (Berzins et al. 1977). Less noble and thus more reactive aluminum alloys (higher corrosion potentials) are more susceptible to this form of corrosion (Ezuber et al. 2008). Experimental observations suggest that aluminum corrosion is most significant during the first week of submergence, with rates inversely correlated with exposure time (Al-Moubaraki and Al-Rushud 2018; Berzins et al. 1977; Dexter 1980; Ezuber et al. 2008; Nişancioĝlu 2007). This decrease in corrosion has been attributed to the aforementioned oxide later. As aluminum reacts with dissolved oxygen, the patina buildup helps to separate the corrosive redox reactions, as aluminum is no longer in dissolution (anodic reaction, oxidation) (Dexter 1980; Ezuber et al. 2008). Thus, the reduction of oxygen at the cathodic site no longer corresponds with continued release of aluminum ions. All things equal, most aluminum alloys should remain fairly stable in marine environments following the initial submergence. Disruptions to the protective film and sizeable decreases in pH (increased acidity), however, can initiate renewed corrosion, making it difficult to construct linear timelines of decay (Ailor 1974; Féron 2007; Phull et al. 1997).

Corrosion Theory Applied to World War II Aircraft

In the construction of WWII aircraft, pure aluminum (Alclad, ~90%) was only used in the coating of aluminum alloy components (Hendershot 1948; Skrabec 2017). Thus, the complete conceptualization of corrosion related to SAWSs must also consider the influences of the alloying metals, namely copper for Al 2024. This begins with the oxidation of $CuAl_2$, which form in the metal structure during the alloying process. The resulting cuprous oxide (Cu_2O) and aluminum cannot coexist in the presence of chloride ions (MacLeod 1983). This leads to the formation of aluminum oxide and the release of copper ions into solution. Following this reaction, the copper precipitates back onto the object's surface and forms a cathodic site through depolarization (Davis 1999). The replated copper (blue/green corrosion products) increases the efficiency of oxygen reduction at the cathodic site, which accelerates the accompanying oxidation reaction at the anodic site. The presence of copper can also result in a form of corrosion known as intergranular corrosion (Davis 1999; Richards and Carpenter 2015). This occurs at the boundaries between copper and aluminum crystallites (grains), which are crystal structures that form during the cooling period of the alloying process. The aluminum in these areas, due to the metal's highly reactive nature, preferentially corrodes. The result is an anodic site forming along the copper-depleted regions of the grain boundary, while a cathodic site forms at the copper-rich areas. This form of corrosion could be considered galvanic, as the preferential corrosion of aluminum occurs as a result of aluminum in contact with copper, while in the presence of an electrolyte (seawater) (Davis 1999). The overall effect is an increased surface area for corrosion to take place (Richards and Carpenter 2015).

The benefits of copper as an alloying metal in aviation engineering are evident by small amounts of copper (4% of total solution) resulting in dramatic increases (e.g. +85%) in the stress load capacity of aluminum (Judge 1943; MacLeod 1983). This enables aircraft to remain relatively light weight, which is essential for flight, while achieving the mechanical strength necessary for the transportation of crew, munitions, and other components. For these reasons, the main alloy used in aircraft construction (Al 2024) contained the highest percentage of copper amongst the aluminum alloys available during WWII. Unfortunately for UCH resource managers, and evident by the preceding discussion revolving around the effects of copper in marine environments, its inclusion in WWII aircraft construction provides an additional preservation threat to submerged wrecks. Furthermore, there may be environmental concerns about the corrosion of alloys containing copper. Excess amounts of dissolved copper in marine environments can be fatal for several types of filter-feeding organisms, with toxicity increased by the effects of ocean warming and acidification (Lewis et al. 2016). Bell (2019) also noted increased levels of manganese, iron, nickel, and molybdenum pollution associated with sediment cores taken associated with a submerged PB4Y-2 Privateer wreck (1956) in Washington state.

Corrosion Surveys of Submerged Aircraft Wreck Sites

The only two corrosion studies explicitly focused on WWII SAWSs come from Micronesia in the Pacific. Macleod (2006b) conducted the first study, which investigated the E_{corr} and pH of five Imperial Japanese Naval planes found in Chuuk Lagoon, Federated States of Micronesia (FSM). An overall trend emerged, as E_{corr} rates became less cathodic (i.e. lower-corrosion rate) with depth. This pattern is due to decreasing dissolved oxygen concentrations that correlate with increasing depths, and thus, oxygen reduction at the metal-seawater interface is less prolific. However, MacLeod noted that values often varied locally, which he used to infer information on the different metallic makeups of aircraft components. For example, the E_{corr} of the pure aluminum coating and duralumin structures (e.g. wing, frame, float, fuselage) differed from one another, as well as, from other features, including propellers, anchors, machine guns, and engines. Even more localized, the pH of certain locations indicated vastly different microenvironment conditions related to acidity. MacLeod came to four main conclusions: 1) corrosion studies provide a “nondestructive technique” to understand aircraft metallurgy and decay trajectories, 2) corrosion rates can be reflective of “known supply problems” during the latter parts of WWII, 3) in situ studies can be combined with laboratory experiments and archival documentation on aircraft production to determine treatment and mitigation options, and 4) more studies are needed to produce accurate “corrosion maps,” especially given the effects of localized corrosion.

Richards and Carpenter (2012, 2018) conducted the second study on three US aircraft and two Japanese aircraft associated with the Battle of Saipan. Using the same methodology as MacLeod (2006), Richards and Carpenter estimated copper concentrations based on E_{corr} and pH. They concluded that the TBM Avenger (US) may have the highest copper concentration, which could lead to relatively faster corrosion rates as a result of pitting and intergranular corrosion. Similar to the Chuuk study, the aircraft in Saipan, overall, demonstrated varying degrees of corrosion, both between sites and within a single site. The aluminum alloy surfaces (e.g. the wings, floats, and engine cowlings) were often significantly corroded, exhibiting clear signs of pitting and perforation. The depositional event also appeared to influence the corrosion process. Aircraft that were severely articulated through catastrophic wrecking exhibited increased signs of corrosion, likely owed to increased surface exposure to seawater. A third corrosion survey of the SAWSs in Saipan was performed in 2023 with results forthcoming (Pruitt and McKinnon 2024).

In Chuuk and Saipan, the biological inertness of aluminum (discussed below), as it is often toxic for colonizing organisms (Kamimura and Araki 1984), limited the amount of biofouling. Macrofouling, the presence of organisms larger than microbes, is mainly restricted to features that are higher in iron concentrations. There, corals, sponges, and other benthic organisms are able to establish themselves on a wreck's surface. The main form of biofouling on submerged aluminum is then dominated by bacteria and other microorganisms. This type of colonization often takes the form of biofilms, which are thin, slimy layers that consist of microbes, corrosion products, and adhesive substances. Both MacLeod (2006b) and Richards and Carpenter (2012) note the presence of a "mucilaginous layer" covering areas of the aircraft. Each study also discusses the ability for the microenvironment conditions under this biofilm layer to be highly localized, resulting in differing pH values and corrosion rates. While not explicitly addressed, this assertion is suggestive of a third type of localized corrosion: MIC.

Microbiologically-Influenced Corrosion

Microbiologically-influenced corrosion refers to the ability of microbes to increase corrosion rates through their presence and metabolic activities (Little and Lee 2007; Little and Wagner 1997; Little et al. 1992). Specifically, biofilm and its associated microorganisms alter the electrochemical conditions of microenvironments, which in turn, facilitate the corrosive redox reactions referenced above (Videla and Herrera 2005). This process begins with the adsorption of macromolecules (e.g. proteins, polysaccharides, humic acids), smaller molecules (e.g. fatty acids and lipids), and nutrients to areas along a wreck's surface (Monds and O'Toole 2009). Aerobic microbes in the surrounding environment are then drawn to these areas through chemical clues and other signals. The grain boundaries between copper and aluminum, as well as, oxidized corrosion products that form as a result of generalized corrosion can serve as ideal attachment sites (Sreekumari et al. 2001). As these initial colonizers grow and multiply, they produce an adhesive and protective layer known as extracellular polymeric substances (EPS) (Dang and Lovell 2016). This gives the biofilm its slimy texture and promotes the attachment of additional microorganisms. While the surface of a corroding aircraft has a negative charge, the EPS in biofilm "bridges" negatively charged bacteria to the aluminum (Little and Lee 2007:8). Oxygen gradients form within this layer of biofilm, as the microbes in the outer sections metabolize dissolved oxygen from the surrounding seawater (Melchers and Jeffery 2012). Diffusion of oxygen decreases within the biofilm, until it reaches anoxic or hypoxic levels (Dexter 1987).

Microbiologically-Influenced Corrosion of Aluminum

Before discussing the MIC process as it relates to aluminum, it is necessary to first address the ability of microbes to colonize a seemingly inhospitable metal surface. Despite making up around 8% of the earth's crust (Haynes et al. 2015:14-19), thus a common component of global sediments, aluminum does not appear to have a biological function (Piña and Cervantes 1996). For many bacteria, aluminum exposure can be toxic, akin to the impacts of other heavy metals (Exley and Mold 2015; Haug and Foy 1984; Piña and Cervantes 1996; Robert 1995; Sterrit and Lester 1980). Therefore, aluminum surfaces are often a less favorable substrate for colonization, contributing to the species-sorting process. In submerged environs, the aluminum oxide layer that forms is hydrophobic, which may further influence the ability of microbes to attach (Zhai et al. 2022:6). Yet, biofilms are commonly reported on SAWS and other forms of underwater aluminum, as discussed above. This apparent contradiction is owed to a suite of adaptations, mainly revolving around the cosmopolitan structure of biofilm. Bacteria capable of withstanding aluminum toxicity, whether that be through the production of certain proteins and cellular structures that mitigate the impacts of heavy metal poisoning, enjoy a competitive advantage during the initial colonization period (Appanna and Hamel 1996; Ferreira et al. 2012; Jo et al. 1997; Nies 2003; Piña and Cervantes 1996; Price 2020; Shukla et al. 2017; Wekesa et al. 2022). Through the production of adhesives (e.g. EPS) and other metal-binding secretions (e.g. chelating agents), these pioneering colonizers alter the physio-chemical properties of the aluminum substrate, enabling the attachment of secondary colonizers (Braud et al. 2010; Ferreira et al. 2012; Koechler et al. 2015; Mansfeld 2007; Schalk et al. 2011; Zuo et al. 2005). The "crowded city" conditions help to offset aluminum's biological inertness, allowing for unexpected levels of diversity and symbiotic associations (Booth et al. 2011, 2013; Dang and Lovell 2016; Harrison et al. 2004; Koechler et al. 2015; Mansfeld 2007; Sancy et al. 2015).

Returning to MIC, the presence of marine biofilm affects the corrosion of aluminum in three ways (Dexter 1987; Little and Lee 2007; Nelson et al. 2017). First, the deoxygenated environment created within and under biofilm can prompt increased metal dissolution through the redox reactions associated with an oxygen concentration cell. Essentially, the adjacent areas not under the respiring biofilm colony are depolarized and become cathodic. Consequently, the less-oxygenated aluminum under the biofilm becomes anodic, with electrons moving from beneath the biofilm to the adjoining cathodic sites. This can allow the E_{corr} at a particular location to reach its pitting potential, enabling pit growth as a part of the corrosion process. A similar phenomenon has been observed when microbial communities form tubercle structures rather than a continuous film (Dexter 1987). This can occur on ferrous components of aircraft, where corrosion products formed by iron-oxidizing bacteria (FeOB) take a volcanic-like form. Laboratory experiments by Hardy and Brown (1984) revealed pitting corrosion taking place under tubercles through the creation of oxygen concentration cells.

These varying oxygen concentrations also promote the growth of anaerobic microbes by providing an anoxic refuge and organic waste products from the aerobic biofilm constituents (Dang and Lovell 2016; De Carvalho 2018; Emerson 2018; Finnegan et al. 2011; Oberbeckmann et al. 2016; Zhang et al. 2015). This allows for the second form of MIC to occur, which relies on ecological relationships between clades of microbes. Emerson (2018) posited that in general, this begins for metal surfaces in marine environments with colonization by oxygen-tolerant microbes, including bacteria belonging to the Proteobacteria and Bacteroidetes phyla. It should be noted that the toxicity of aluminum creates can create considerable stress for would-be colonizers, which allows more aluminum-tolerant microbes to outcompete those that are not as well-adapted (Robert et al. 1995). As the biofilm layer becomes denser, oxygen is no longer able to diffuse inwards. This, combined with the organic waste products secreted by aerobic organisms allows for the survival of anaerobic microbes, such as sulfate-reducing bacteria (SRB) and methanogens, within the lowest levels of the biofilm layer (Dexter 1987; Emerson 2018; Ghali 2010).

Sulfate-reducing bacteria (SRB) are of particular interest due to their ability to alter electrochemical conditions at the wreck surface and their production of sulfides, which readily react with metal surfaces (Iverson 1966; Postgate 1979). Rather than referring to a specific class or other taxonomic ranking, SRB refers to a functional group of bacteria comprised of numerous taxa who possess the ability to respire using sulphate as an electron acceptor. Barton and Fauque (2009:44) note that more than 220 species of SRB have been described, encompassing a total of 60 genera. The majority of these taxa fall within the Deltaproteobacteria class, though the gram-positive SRB generally belong to the Clostridia class (Muyzer and Stams 2008). These anaerobic microbes have been isolated from both seawater and marine sediments, which explains how their inoculation into established biofilm colonies (Hardy and Hamilton 1981). Sulfate-reducing bacteria utilize naturally-occurring sulfate (SO_4^{2-}) in the water as the aforementioned terminal electron accepter and the organic waste products as the electron donor (Hamilton 1985). Guan et al. (2017) offered the following equation as a possible mechanism for the effect SRB have on the corrosion of aluminum alloys:

$Al3^{+} + HS^{-} + OH^{-} \rightarrow Al_2S_3 + H_2O$ (1)

$Al_2S_3 + H_2O \rightarrow Al(OH)_3 + H_2S$ (2)

Here, the corroding aluminum at the anodic site (i.e. beneath the biofilm) reacts with the hydrogen sulfide and hydroxide produced by the reduction of sulfate to form aluminum sulfide. The hydrolysis of the aluminum sulfide then results in aluminum hydroxide (corrosion product) and hydrogen sulfide gas. Thus, the ability of SRB metabolites, namely HS^- to readily react with aluminum and promote further dissolution, is a potential pathway for MIC of SAWSs. The overall relationship (Figure 1.3) can be summarized as:

$Al + SO_4^{2-} \xrightarrow{\text{SRB}} Al(OH)_3 + HS^-$ (3)

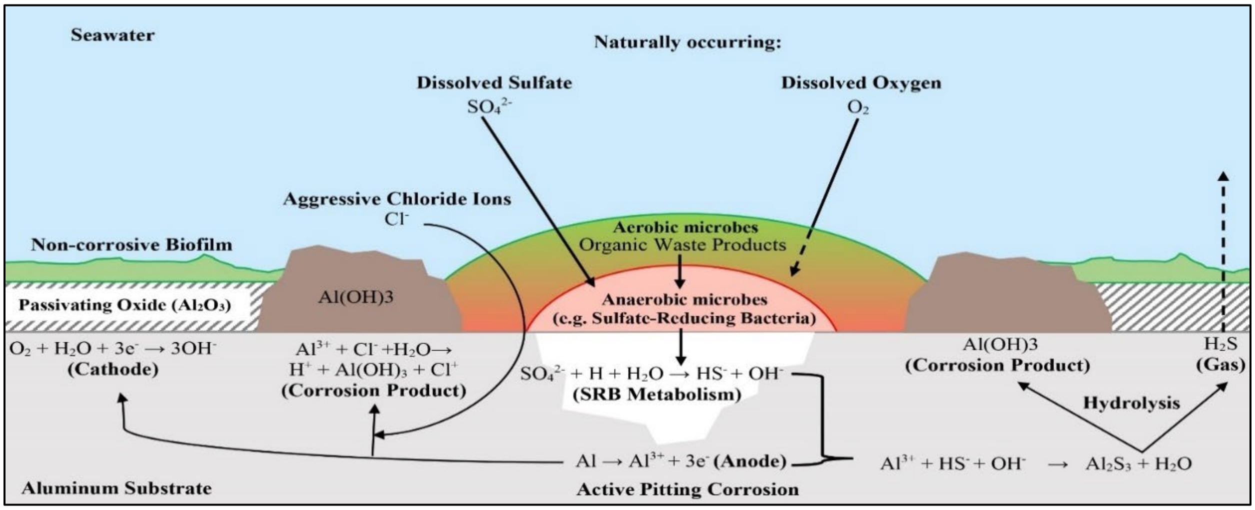

Figure 1.3. Diagram of microbiologically influenced corrosion of aluminum depicting both pathways. Illustration by the author. Left: Differential Aeration Cell; Right: Reactive Metabolite Production. (Includes information from Dexter, 1987; Guan et al., 2017; MacLeod, 1983.)

The prevalence of SRB in sediments constitutes an important point to consider when assessing in situ preservation strategies, especially reburial. Liu et al. (2014) found that SRB were responsible for significantly increased corrosion for aluminum alloy anodes buried in marine mud from Jiaozhou Bay, China. Other microbes, namely marine fungal species, have also been associated with active corrosion of aluminum through the production of acidic metabolites and disruption of the protective, oxidized film that forms on submerged aluminum (Dai et al. 2016; He et al. 2022; Lee et al. 2014; Silva et al. 2007; Wang et al. 2019; Zhang et al. 2022, 2023). The latter enables increased attacks from chloride ions, leading to an accelerated corrosion process (Dexter 1987; Nelson et al. 2017). Finally, the EPS and other exopolymers produced by microbes in biofilm can have the ability to trap and bind to metal ions (Azeredo and Oliveira 2000). This can create cathodic sites, akin to the precipitated copper previously mentioned, further accelerating the corrosion process as aluminum preferentially corrodes through the donation of electrons.

Microbiologically-Influenced Corrosion in Underwater Archaeology

While SAWSs have yet to be the subject of MIC research, there exists a burgeoning corpus of literature regarding the effect MIC has on UCH resources. Reviewing this information not only places the current dissertation within the context of what has already been conducted, but invites speculation on how future MIC studies can be applied to SAWSs. Additionally, there has yet to be a comprehensive synthesis of MIC in UCH contexts, despite the multitude of studies that focus on this topic. Thus, the following is also intended to serve as a resource for those who may come across this dissertation while researching MIC and archaeology.

Interest in the MIC of steel shipwreck coincided with the discovery of the RMS *Titanic* wreck, where meter-long iron accumulations, termed “rusticles” (Ballard 1987), were noted on the outside of the ship. The rusticles' iron composition initially compared favorably with that of corrosion products taken from the ship's hull, resulting in the assumption that the rusticles were proof of the wreck's deterioration (Cullimore and Johnston 2001). Further connections between rusticles and corrosion were made following the identification of reducing conditions and certain bacterial communities within rusticles, which sparked concerns about "biological extraction" (Cullimore et al. 2001:126). Cullimore and Johnston (2001) posited that bacteria colonizing *Titanic*'s surface were consuming iron ions directly from the hull, forming rusticles through the oxidization process. The authors estimated that between 47.45 – 73.0 tons of *Titanic*'s metal were lost annually. The popular press was fond of reporting Cullimore and Johnston's overall conclusion that *Titanic* could be lost within 280 – 420 years (Ella 2001). Efforts were then made to characterize the specific microbial taxa responsible, which consistently identified iron-oxidizers and SRB within rusticle samples (Stoffyn-Egli and Buckley 1995; Cullimore et al. 2001:126; Cullimore and Johnston 2008). To empirically ascertain the decay rate, experimental steel coupons placed near the wreck, which indicated a metal loss of 0.03-grams/centimeter^2 (cm) per year over a 6-year period (Cullimore and Johnston 2008**)**. More recently, the isolation of a novel bacterial species, *Halomonas titanicae*, from *Titanic* rusticles has caught the attention of MIC researchers (Sánchez-Porro et al. 2010; Dong et al. 2020; Li et al. 2022). This gram-negative, halophilic bacterium uses rust to gain energy in the form of electrons from iron degradation (Sánchez-Porro et al. 2013). The exact role *H. titanicae* plays in the corrosion of *Titanic* remains debatable, as it was recently shown in laboratory tests that in the presence of *H. titanicae*, steel corrosion was inhibited under aerobic condition but accelerated under anaerobic condition (Wang et al. 2021).

The Gulf of Mexico (GOM) proved to be an especially fertile ground for pursuing MIC research. A multi-year assessment of six WWII ships revealed that the wrecks were covered by substantial biological growth (e.g. microbial rusticles formations, biofilms, and microbial concretions) (Church et al. 2007, 2009; Church and Warren 2008). The on-site observations were paired with the deployment of test coupons at each wreck and an analysis of recovered concretion and rusticle samples (Overfield 2005). These efforts led to conclusions regarding "clear evidence that the investigated ships are deteriorating as a result of biological activity extracting iron from the ship's steel hulls" (Church et al. 2007:206). Key inter-site differences were also noted, highlighting the role that environmental factors, like depth, exposure to dissolved oxygen, nutrient availability, and competition from macroorganisms, play in shaping wreck microbiomes.

Some researchers, however, have pushed back against the notion that the presence of specific types of bacteria within rusticles is sufficient evidence to assume MIC. Relying solely on spatial relationships ignores other important considerations, chiefly the need for a corresponding cathodic reaction with the supposed anodic dissolution of a wreck by microbial activity. For example, Salazar and Little (2017) provided evidence of this faulty assumption when re-examining the *Titanic* rusticles, concluding that the lack of an identifiable cathodic reaction and the presence of environmentally-available iron likely indicated that the rusticles were formed through the abiotic accumulation of iron as opposed to the extraction of iron from the ship by microbes. In other words, the rusticles were not a result of biodeterioration, but instead, an ideal, iron-rich substrate that played host to a consortia of aerobic iron-oxidizers and anaerobic sulfate-reducers. Little et al. (2019:5) also reassessed archived materials, finding that "[t]he physiochemical properties of rusticles from GOM shipwrecks are not consistent with the mineralogical layering typical of Fe corrosion products," and encouraged others to seek the environmental (abiotic) factors influencing rusticle formation.

Beyond rusticles, the MIC of shipwrecks has been examined more recently in the context of oil spills (Hamdan et al. 2018; Mugge 2018; Mugge et al. 2019a, 2019b, 2021; Salerno et al. 2018). A sudden influx of hydrocarbons and dispersal chemicals is likely to affect the composition of microbial communities. The Deepwater Horizon spill offered an opportunity to evaluate this hypothesis and assess changes to sites within the impacted area. Researchers have confirmed the ability of crude oil, dispersed crude oil, and dispersant to measurably impact the microbial community composition of seawater and steel-surface biofilms, including the proliferation of known bio-corroders (Mugge 2018; Salerno et al. 2018). Metal coupons placed on sites both within the spill plume and outside of it also revealed noticeable differences in microbial recruitment and gene abundances (Mugge et al. 2019a). Loss of metal was higher for coupons within the spill's footprint, supporting previous conclusions based on experiments testing microbial influence on corrosive reactions and the functional response of microbes to the aforementioned pollutants (Mugge et al. 2019b). Additional analysis suggested that the sediment was the main contributor of taxa to the coupon biofilms from sites within the spill area, highlighting a way in which the spill's environmental impact continues to affect wreck microbiomes (Hamdan et al. 2018; Mugge et al. 2019a). The 'micro-scale impacts' revealed during laboratory studies and the on-site ecological data were used to explain real-world observations of wreck impacts. Most notably, time series imagining, including recent acoustic scanning and 3D documentation, indicated that the WWII German U-Boat U-166 had undergone significant deterioration since the spill (Damour et al. 2016).

Recent research has revealed that shipwrecks can, in turn, effect the composition of surrounding sedimentary microbiomes. Acting as an ‘island’ or ‘oasis,’ shipwrecks not only draw their own unique microbiome, but have measurably influenced the microbial composition of the sediment, up 200 meters (m) from the site, through the creation of a halo-like ‘transition zone’ (Hamdan et al. 2021). The introduction of a sizeable substrate can trigger the familiar process of biofilm formation, growth, and eventually dispersal, where bacterial colonies are introduced to areas adjacent to the wreck. Substrate material was recently proven to be a prominent factor in determining the taxonomic composition of the biofilm communities that reform on built structures near wrecks (Mugge et al. 2023a, 2023b). Thus, the dispersal of microbial communities, and their subsequent inoculation into biofilms on seafloor infrastructure (oil rigs and pipelines), has drawn considerable interest from those wishing to minimize the occurrence of MIC. Some have noted that the influence shipwrecks have on benthic microbial communities is more pronounced in deeper areas, where there are less viable substrates and lower nutrient concentrations (Hamdan et al. 2021; Hampel et al. 2022; Moseley 2021; Moseley et al. 2022).

There are, of course, ecological concerns about the ability of shipwrecks to influence microorganisms, particularly when that ability is linked to fuel leakages. Microbial concentrations have been observed growing on or near ship oil on numerous occasions, including *Maru* in Chuuk and USS *Arizona* (Russell et al. 2004; MacLeod et al. 2017). For HMAS *AE2*, a WWI submarine wrecked off of Turkey, “large black mats of biological growth” were observed and described as the “by-products of the microbiological attack on diesel fuel” (MacLeod 2019:874). Thomas et al. (2021) assessed whether obligate hydrocarbonoclastic bacteria could be found in microbial communities surrounding the HMS *Royal Oak* wreck off Scotland. If community structure has been fundamentally altered by the escaped fuel diffusing into the benthic environment, it should be evident by the taxonomic legacy left behind. While this was not evident for the Scottish study, Van Landuyt et al. (2022) reported strong taxonomic affiliation between sediment samples with increased aromatic pollution and known hydrocarbon degrading bacteria.

Besides oil spills, other anthropogenic influences on the taxonomic composition of wreck microbiomes have been noted, including the availability of nutrients, particularly dissolved inorganic nitrogen (DIN) (Gu 2012; Little and Lee 2014; Melchers 2013, 2021). Considered to be a limiting nutrient in seawater, DIN is vital to the microbial metabolic activities involved with MIC (Little and Lee 2007; Melchers 2018; Melchers and Jeffery 2012; Melchers and Lee 2021). Just as the introduction of hydrocarbons to a marine environment can be inferred as having a negative effect on metallic UCH due to the influence on microorganisms, so can elevated DIN levels. Melchers (2014) proposed DIN measurements of ambient seawater can serve as a proxy for estimating MIC levels. Sites in DIN-rich waters, a result of contaminated runoff and other sources of pollution, are thus expected to have higher microbial action across the spectrum, including the metabolic activities responsible for MIC. USS *Arizona*, where microbes detected within corrosion products were thought to possess "an important role in the continuing corrosion of the USS *Arizona*," stands out as example of a threatened resource (McNamara et al. 2009:232). The oil pollution and other contaminating nutrients (i.e. DIN) associated with an active naval yard such as Pearl Harbor, has caused those tasked with monitoring *Arizona*'s preservation to further consider how microbial activity may be continuing to influence corrosion.

Several recent studies aimed at directly characterizing the microbiome collected from UCH resources. In Nigeria, researchers carried out a qualitative assessment of bacterial activities within shipwrecks within the Iwafe Estuary, noting the presence of three key taxonomic groups collected from rusticles and other corrosion products (Olukole et al. 2020). A more quantitative approach was taken in North Carolina, in which the taxonomic composition of microbial samples from the wreck of LCS-123, a WWII landing craft, were compared to that of sediment and water samples (Price et al. 2021). Results indicated that shipwreck samples were more similar to one another, as compared to the environmental samples, though notable differences between samples from non-corroded and visibly corroded wreck surfaces were observed. from steel-wrecks The latter was evident by increased FeOB abundance within corroded samples, suggesting that either these bacteria were actively influencing corrosion, or the corroded areas served as preferential attachment locations. Furthermore, the iron-oxidizing Zetaproteobacteria *Mariprofundus ferrooxydans* O1 was isolated directly from the steel-hulled shipwreck, which supported the notion that MIC organisms could be associated with site corrosion. Van Landuyt et al. (2022) also noted a relatively high abundance of suspected biocorroders, including SRB, affiliated with biofilm samples obtained from a WWII-era shipwreck site off Belgium.

Off the coast of western Australia, the WWII shipwrecks HSK *Kormoran* and HMAS *Sydney* offered another glimpse into the intersection of microbial activity and the corrosion process. Using scanning-electron microscopy (SEM), "mineralized microbial structures" were observed within the shipwrecks' corrosion products, which led the authors to conclude "that microbial activity on iron -hulled structures is a significant process in deep-sea environments… [and] these microorganisms and their metabolic by-products are expected to affect the composition of corrosion products" (Albahri et al. 2019:1995)**.** In the North Sea, off the coast of Belgium, researchers used the microbiome of a submerged steel chain as a proxy for shipwreck sites in the vicinity. Low microbial concentrations from corrosion samples and an absence of identifiable MIC products suggested that "MIC is likely to be irrelevant for shipwreck corrosion in this part of the North Sea" (De Baere et al. 2019:11). The differences between the MIC of wrought iron, cast iron, and mild steel were explored in Chuuk (MacLeod et al. 2017). Iron phosphide inclusions within both iron substrates enabled anaerobic bacteria, such as SRB, to produce essential nutrients (e.g. phosphines), though this was greatest for cast iron. The authors called for attention to be paid to the type of iron and conclusions regarding MIC be made on the basis of comparisons between iron of the same nature.

While SAWSs have yet to be the subject of MIC research, studies examining the role of microorganisms in the corrosion process have expanded to other UCH resources. Again, in Western Australia, Usher et al. (2014) used pyrosequencing to characterize the microbiomes associated with tubercles found on the corroded surfaces of a WWII-era steel railway line submerged in 0.5 m of water. *Methanococcus maripaludis*, a known biocorroder through its consumption of electrons from steel substrates, dominated these assemblages and led researchers to conclude that corrosion was indeed being driven by microbial activities. Due to safety concerns and potential environmental impacts, sunken munitions have also been the topic of recent corrosion research. Chock and Silva (2016) confirmed the presence of "skirt-like" corrosion products on several unexploded ordinances in a dumping ground near Pearl Harbor. Though the authors attributed their formation to microbial activities, the inability to collect physical samples precluded confirmatory microbiological analysis. Finally, a multiyear study aimed at discerning the cause of increased corrosion of submerged munitions pile in the Baltic Sea identified large concentrations of SRB within sedimentary samples taken from under the explosives relative to control sediment samples, which provided a plausible link to MIC (Cybulska et al. 2020).

Project Setting

The preceding discussion illustrates the diversity of impacts that UCH sites and the microbial environment can have one another. To extend this line of research to the previously unexplored microbiomes associated with SAWSs, four sites in the waters around the Hawaiian Islands of Maui and Oʻahu were chosen as study sites. The original dissertation proposal, however, called for a trans-Pacific comparison between the two Maui aircraft and two SAWSs in Saipan, Commonwealth of the Northern Marianas Islands (CNMI). Due to the CNMI's travel restrictions associated with the 2020 COVID-19 Pandemic, the decision to focus solely on Hawaiʻi was made.

The wrecks were chosen in consultation with the ONMS, which maintains the ILSCR. Sites were chosen based on the following criteria: 1) depths within 25 m; 2) located in a publicly-accessible area; and 3) sufficient aluminum surfaces remaining. Upon combing the list of SAWSs with verified locations, two sites in Maui's Māʻalaea Bay and two sites in Oʻahu's Waimānalo Bay were selected (Figure 1.4). The former consisted of a Curtiss SB2C-1C Helldiver and a Grumman F6F-3 Hellcat (Figure 1.5). The bay itself serves as the southern bight of Maui, separating West Maui from the slopes of Haleakala to the east. The arching shoreline is mainly white sand beaches overlying volcanic bedrocks. The offshore environment is also predominantly sandy, with limited coral growth and patches of seagrass. The gradually-sloping seafloor bottoms out around 30 m at the entrance to the bay, though several shoaling areas interrupt this progression. Māʻalaea's level bathymetry generally precludes significant wave action within most of the bay, though wind-driven swells, particularly during the summer and fall, can cause rough surf conditions at the surface. Water temperature tends to be around the average for Hawaiʻi (25°C) with little seasonal fluctuations (Moberley et al. 1963:49).

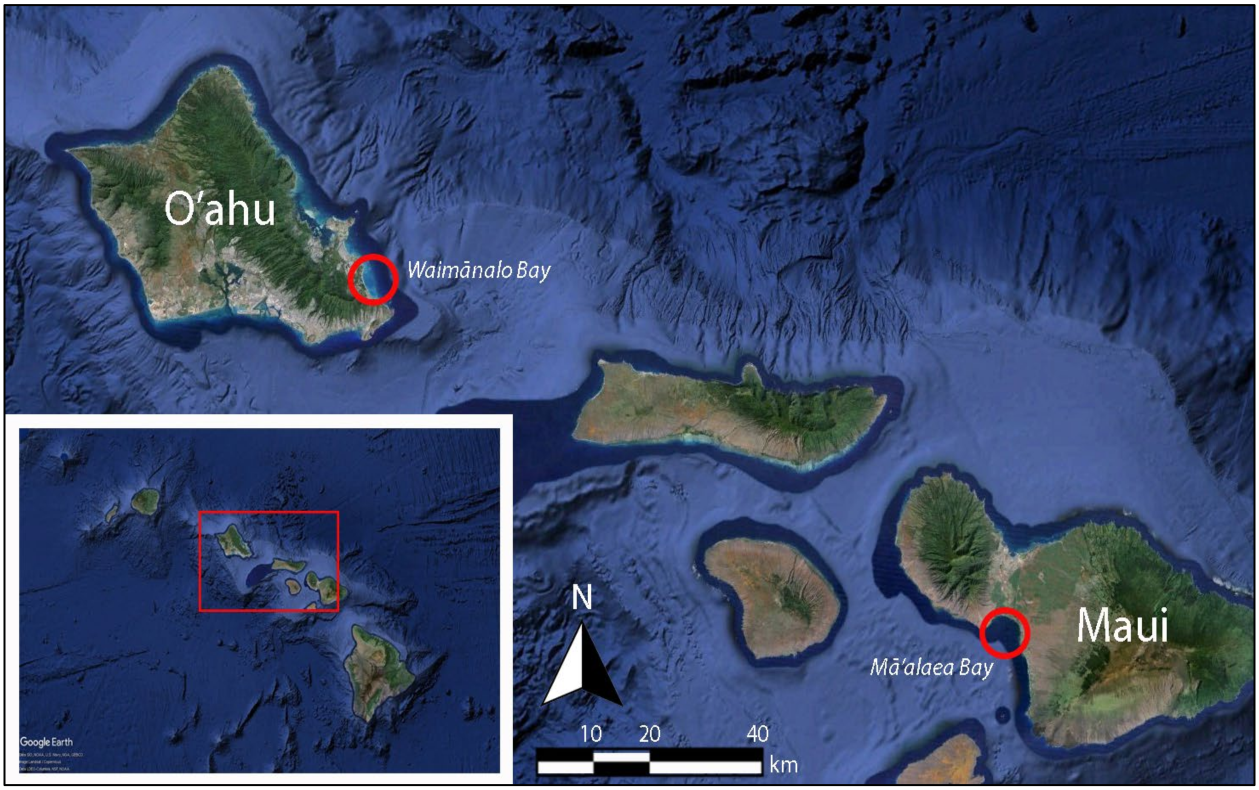

Figure 1.4. Map of the study area with fieldwork locations indicated. (Imagery courtesy of Google Earth)

On 11 December 1941, the USN requisitioned the civilian Maui Airport, commissioning it as Naval Air Station (NAS) Puunene (DON spelling). Located only 3 km from the Mā‘alaea shoreline, the USN stationed several squadrons at Puunene, including Carrier Aircraft Service Unit 4, Fighter Squadron (VF) 72, and Utility Squadron 11 (Cotton 1945). Numerous other units conducted training activities at Puunene, resulting in an estimated 106 squadrons and carrier air groups passing through during the war’s duration (Cotton 1945). Following the initial Pacific Campaigns, veteran aviators returned to Puunene with invaluable lessons to share. Those with experience taught ‘green’ pilots tactics specific to engaging with Japanese Zeroes, while bombing operations became a point of emphasis later in the war (PHAM 2023). Departing from both Puunene and offshore carriers, bomber crews executed attacks on simulated Japanese defensive positions. Following its development in 1943, Maui became a fertile testing ground for understanding the technological superiority of the F6F Hellcat (Andrews 1988).

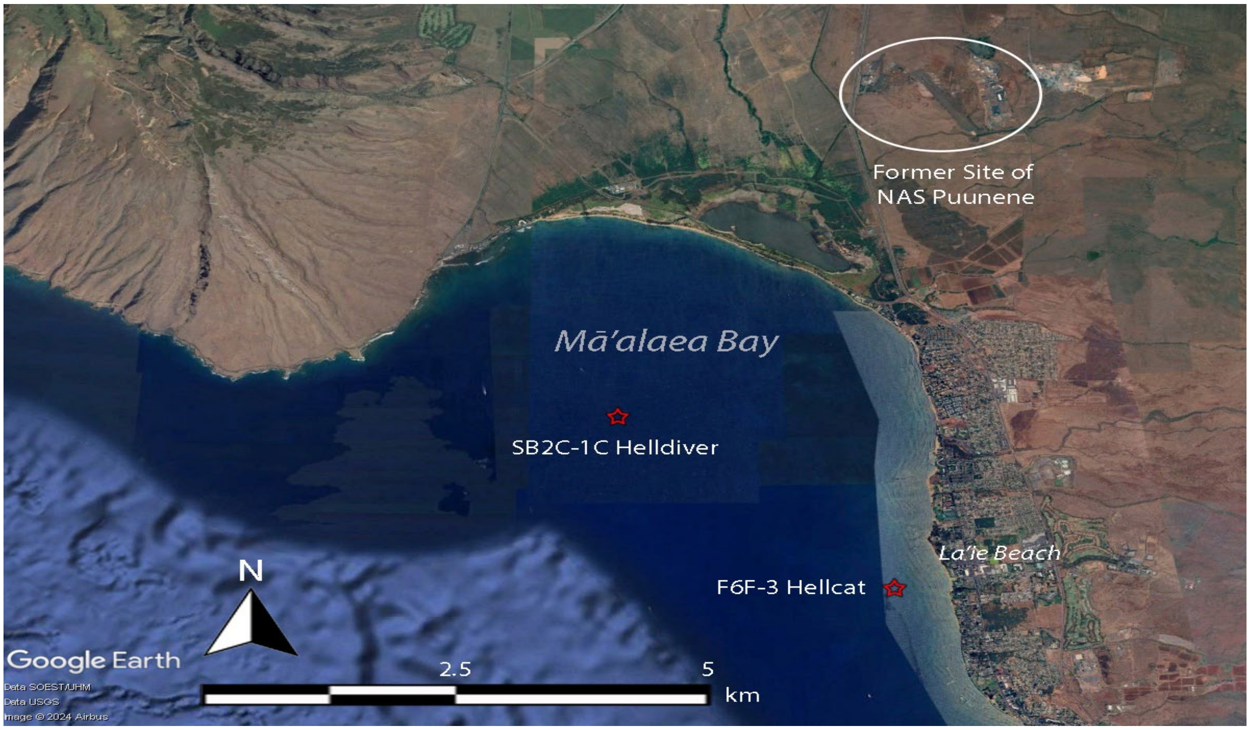

Figure 1.5. Map of Māʻalaea Bay, Maui with site locations indicated. (Imagery courtesy of Google Earth)

The Oʻahu sites consist of a Republic P47 Thunderbolt and the wing of a suspected Goodyear FG-1A Corsair. These wrecks are located at opposite sides of Waimānalo Bay (Figure 1.6). Lacking the pronounced curvature of Māʻalaea, Waimānalo is an east facing bay that affronts a wide valley. Situated between two rocky headlands (Wailea Point and Makapuʻu Point), the white sand shoreline is composed of very fine, calcareous grains and constitutes Oʻahu's longest continuous beach. The sandy shoreface eventually gives way to a series of large reef flats and sand pockets. For about 2 km, depths in the bay are consistently shallow (2-4 m), before dropping off to about 7-9 m beyond the 2 km mark. Water temperatures remain fairly stable throughout the year, ranging between 23-27°C. Though the eastern Oʻahu does not experience the same wave energy that has made the island's northern and southern shores surfing destinations, wrap-around swells from both directions and onshore breezes can roughen the waters (Moberley et al. 1963:32-33).

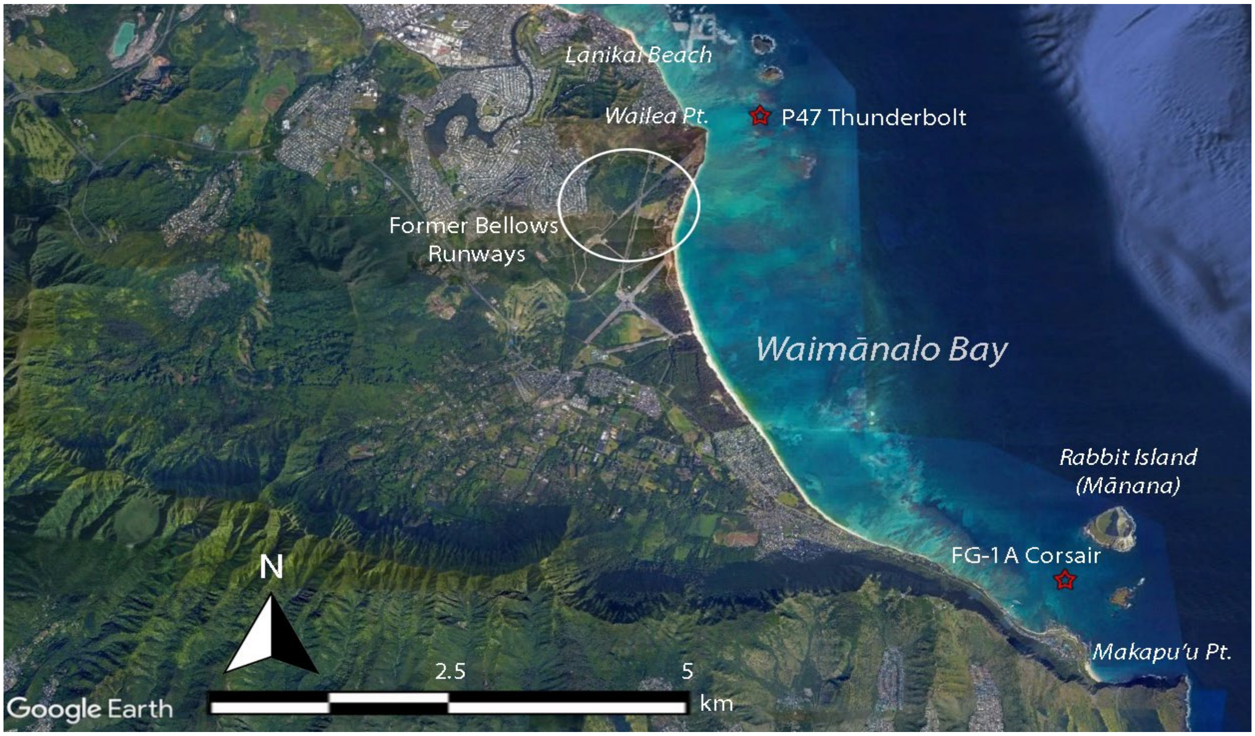

Figure 1.6. Map of Waimānalo Bay, Oʻahu with site locations indicated. (Imagery courtesy of Google Earth)

Like Māʻalaea, Waimānalo was also once the site of considerable military action during WWII. On 7th December 1941, the USAAF Bellows Air Base, occupying much of the northern area immediately inland of the bay shoreline was one of several ancillary targets of the Japanese military's attack (Arakaki and Kuborn 1991). After being put back into operation on 11 December 1941, Bellows operated throughout the war as both an aviation training base and basic training center for new recruits (McGee et al. 2003). As the war's end approached, Bellows became a vital practice area for Very Long Range (VLR) flights, with pilots launching from one of Bellow's three runways in preparation for escort missions targeting mainland Japan (McGee et al. 2003). Additionally, the Waimānalo Amphibious Training Center (WATC) was established nearby. There, "Army and many Navy construction units" of the Central Pacific Base Command "were given a pre-shipboard course of instruction" (Richardson 1946:184). The area was also used by USN Underwater Demolition Teams as an amphibious operation training area, conducting trial detonations and navigating submerged obstacles (NOAA 2017:116).

Site Descriptions

The two Maui aircraft were both surveyed in 2011 as part of a joint-collaboration between the NOAA ONMS and the University of Hawaiʻi, Mānoa (NOAA 2011), and then again in 2022 as part of the Ocean Exploration Trust's "Shore-to-the-Abyss" expedition (Bush et al. 2023). The Curtiss SB2C-1C Helldiver, located in the center of Māʻalaea Bay, lies on an empty, sandy seafloor in about 20 m of water (Figure 1.7). The aircraft is almost entirely intact, which made its identification in 2011 fairly easy (ONMS 2011). The site's remarkable condition makes it perhaps the premiere SAWS in Hawaiʻi from a recreational standpoint and one of the best preserved planes in the entire Pacific. Its easily accessible location in the bay, combined with a depth well within recreational limits, have contributed in making the Helldiver wreck a popular SCUBA diving attraction. The most notable damage has occurred in the front section of the plane, where the engine has slightly broken off from the airframe and the cowling rests on the seafloor to the starboard side. An aluminum panel on the starboard side of the nose has also fallen off, exposing the engine bearing struts. The vertical tail stabilizer is detached and partially buried aft of the wreck. Both the port wing aileron and port elevator have disappeared, while some of the aluminum sheeting on the horizontal tail stabilizer and starboard elevators have worn away. The wreck contains considerable coral growth, especially on the tail, top surfaces of the fuselage, and engine block. In the absence of natural features with vertical relief, the site supports a rich marine biota, including various reef fish, crustaceans, and benthic invertebrates.

Figure 1.7. 3D photogrammetric model of SB2C-1C Helldiver site in Maui. One meter scale bar aft of the aircraft's tail. (Model by the author, 2022)

After its discovery in 2010 by a local dive operator, the Helldiver's Bureau Number (184000) was identified on the detached vertical stabilizer. The NOAA ONMS website for the 2011 survey provides a description of the crash incident:

> "On August 31 1944, pilot William E. Dill and radioman Kenneth W. Jobe, members of patrol bomber squadron VB-4, were conducting dive bombing practice. During evasive maneuvers following their second steep dive on the target, the entire vertical tail assembly twisted to port, jamming the rudder controls. No longer able to safely control the aircraft, and unable to make the runway at Pu`unēnē, the pilot made a forced water landing approximately 1-2 miles south of the Naval Air Station. Both pilot and radioman were rescued."[13]

This series of events is also responsible for the plane's missing rescue raft and why both the pilot's and radioman's canopies are open. The story of the crash is now memorialized on an interpretive plaque that was recently placed at the site.

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[13] https://sanctuaries.noaa.gov/maritime/expeditions/maui/results.html

The Grumman F6F-3 Hellcat, located 4 km southeast of the Helldiver, lies just 600 m from the Laie Beach shoreline (Figure 1.8). The wreck is in 9.5 m of water, surrounded by sand and patches of seagrass. While its proximity to the shoreline allows the site to be well within reach of recreational divers, site visitation is far less common than at the more-complete Helldiver. The Hellcat is known to be accessed by local divers, but thus far, remains mostly absent from dive operator websites and advertisements. The site is divided into two main components, with the first consisting of the midsection of the plane's fuselage and the attached proximal ends of both wings. This part of the aircraft is upside down, making visible the retracted landing gears. Some of the wing's aluminum skins, especially on the portside, have deteriorated away, exposing the ribs. Like the Helldiver, this site also serves as both a substrate for coral colonies and shelter for fish.

Figure 1.8. 3D photogrammetric model of F6F-3 Hellcat site in Maui. Engine section not pictured. One meter scale bars. (Model by the author, 2022)

Around 22-23 m away, the radial engine (cowling missing), propellor, and nose ring can be found intact and standing upright. Sediment covers this section starting from just below the propellor hub, rendering two of the propellor blades and the bottom third of the engine unexposed. The third propellor blade is broken in half and extends vertically into the water column. Like most ferrous components in this environment, the engine is heavily encrusted in coral. During the 2022 survey, divers recognized what appears to be either the distal end of one of the wings or one of the tail stabilizers is buried 5 m away. While the landing fear configuration, engine, and exhaust flaps all led to the identification of the site as an F6F-3 Hellcat in 2011, the specific identity of the plane is unknown. Naval records indicate that at least 39 planes of this model sank in the vicinity of southern Maui (NOAA 2011).

The first O‘ahu site, a P47 Thunderbolt, is located 700 m off the tip of Wailea Point and approximately 1 km from the end of Bellows runway (Figure 1.9). The site’s proximity to the shoreline, and specifically one of O‘ahu’s most popular beaches (Lanikai), has enabled the site to become a frequented recreational attraction. Serving as a popular destination for kayakers, the wreck lies within 4 m of water, and thus easily accessible to both snorkelers and divers. During low-tides and increased swells, however, the mixture of exposed reef and waves can preclude site access, especially during the winter months. Similar to the Hellcat site, the aircraft has separated into two sections, as the engine and propellor have broken off from the body of the plane. The fuselage, with both wings still attached, rests within a narrow clearing in the reef flat, with both the rear of the plane and its nose being propped up by rocky outcrops. The port wing has fallen into a sand pocket, causing the wreck to list towards that side. Much of the wings’ aluminum skins have deteriorated away, exposing ribs and spars. The plane’s machine guns have been removed and the panels over both gun bays and the joining ammunition troughs are missing. Both wingtips have broken off just beyond these troughs. The canopy is absent with the exposed cockpit filled with miscellaneous aircraft debris and the pilot's chair. Forward of the cockpit, the fuselage's forward structure, which housed the fuel tanks, remains intact and terminates at the firewall.

From there, panel-less frames of the nose cone and the engine bearer struts extend until the missing engine cowling. There is a small debris field within the sand pocket on the port site, with the semi-monocoque framing of the fuselage's aft section and attached supercharger clearly identifiable. A full inventory of the aircraft parts onsite has yet to be completed. The engine itself, along with the propellor and cowling, are approximately 8 m away. The aft end of the cowling is propped up, while the bottom two propellor blades are dug into the seafloor. Each of the four propeller blades is noticeably bent. Several aluminum panels of the cowling have fallen away, exposing the aircraft's 18-cylinder twin engine.

Petrey et al. (2008) were the first to archaeologically investigate this site, basing its identification as a Thunderbolt based on the 4-blade propellor and blunt nose, which supported a highly-diagnostic air intake. The wreck, however, has long been known to local residents, serving as a snorkeling spot and an underwater landmark for spearfishermen. Using the available crash records, the authors identified four Thunderbolts that crashed in the ocean near Bellows Airfield. The most likely candidate for this wreck, is a Thunderbolt with the serial number 43-25601, flown by 1st Lieutenant William H. Spark. On 21 June 1944, the pilot reportedly experienced catastrophic engine failure shortly after takeoff on a VLR practice flight. He was able to complete a successful water landing around 1000 m off the end of the Bellows runway, before being rescued by local fishermen according to eye-witnesses (Petrey et al. 2008).

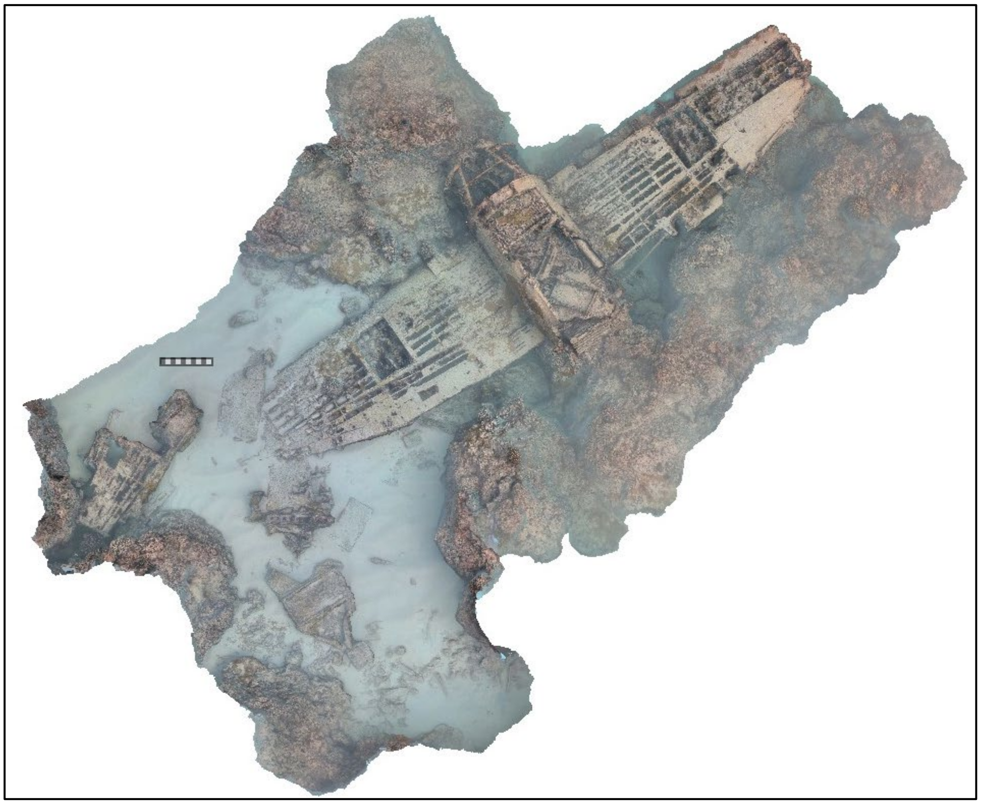

Figure 1.9. 3D photogrammetric model of P47 Thunderbolt site in O‘ahu. One meter scale bar has been superimposed for better visibility. (Model by the author, 2022)

The final site investigated in this study, the suspected FG-1A Corsair, is the least complete of the four wrecks. The highly-fragmented plane is scattered over an area of .05 km^2, 750 m off the adjacent coast and 2 km northwest of Makapu‘u Point. The site currently sits between Manana Island (Rabbit Island) and the Waimānalo shoreline. Depth at the site ranges between 7-11 m, and the seafloor is characterized by a mix of sand and low-lying reef patches. The area is prone to strong water movements, as waves and currents converge on the adjacent headland (Makapu‘u). Locally-known as a hazardous location, the site is essentially neglected by the recreational diving community. One of the wings, believed to be the port side, and the engine are the only definitively identified sections. The wing had been investigated previously in 2013 by UH’s Hawai‘i Undersea Research Laboratory and more recently by a local non-profit, Naval Exploration and Research Divers (NERD) (Figure 1.10). Based on data obtained by the latter

(Marionneaux et al. 2021), the wing possesses several diagnostic characteristics, including the 5-hole reinforcement rib, rounded wingtip, and folding-wing joint. The orientation of the gun ports in relation to the angle of the leading edge suggests that the wing is upside down. Much of the wing's aluminum skins have disappeared, exposing ribs and spars that are consistent with a Corsair in terms of both number on configuration. The fabric skin aft of the main wing spar, a known Corsair feature, has deteriorated away. There is considerable coral growth on the wing, especially the proximal end, despite the fact that the wing is known to buried in sediment for parts of the year. Almost 100 m south, NERD discovered the engine, along with the propellor hub, tailwheel, and .50-caliber machine gun amongst the debris field. The central wing box and horizontal stabilizer have also been tentatively identified by NERD in areas east and west, respectively, of the wing section (Marionneaux et al. 2021).

From its original discovery, the Corsair site has remained uncorrelated until recently, when background research for a NHHC Special Use Permit report associated with this dissertation revealed a possible identity. Aircraft crash records indicated that a Corsair (Bureau Number 14151) wrecked in a location given as "between Rabbit Island and Oʻahu," near Makapuʻu Point. With no other reports of incidents involving Corsairs with similar locational descriptions, confirmation of the plane's identity is awaiting verification by the NHHC. It should be noted that 14151 is given the FG-1A designation, signifying that the aircraft was manufactured by the Goodyear Aircraft Corporation and not the F4U designation associated with the primary Corsair manufacturer, Vought. All 4,007 FG-1 Corsairs, however, were built to the same specifications as the F4Us (Sullivan 2010:8).

According to USN Accident Reports, on 10 October 1945, five weeks after Japan's surrender in WWII, an FG-1A Corsair (14151) piloted by Lieutenant (Lt.) Herbert J Lewis Jr.

collided with Lt. C. William Schlenz's FM-2 Wildcat (47307) near Makapuʻu Point during a routine practice flight. The highly fragmented state of the Waimānalo Corsair site may be evidence of this violent wrecking event. Both men were assigned to the Headquarters Squadron of the 3rd Marine Aircraft Wing stationed at Marine Corps Air Station Ewa in western Oʻahu. While Lt. Lewis was able to safely ditch his aircraft, Lt. Schlenz was killed during the accident. His body was recovered and originally buried at the Hawaiʻi Naval Cemetery, before being repatriated to his hometown of Wyckoff, New Jersey in 1947. Lieutenant Schlenz's Wildcat has yet to be relocated and represents one of two 1945 FM-2 Wildcat wrecks positively associated with Oʻahu (NOAA 2017:179).

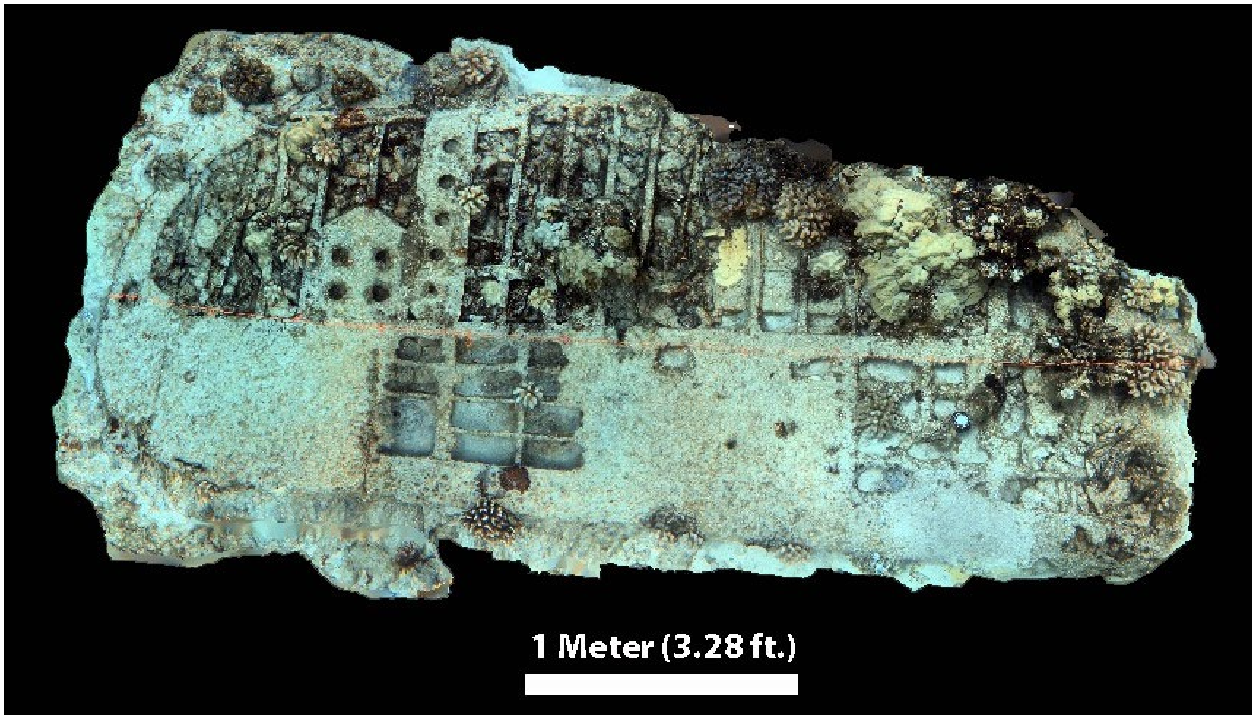

Figure 1.10. Photomosaic of suspected FG-1A Corsair wing. Photos courtesy of Adam Kordish, Naval Exploration Research Divers, 2019. (Photomosaic created by the author, 2022)

Project Objectives and Hypotheses

The primary objective of this dissertation was the characterization of the microbiomes associated with biofilms from the four SAWSs in Hawaiʻi described above. Using DNA sequencing, the microbial community data, including overall diversity and the relative abundance of certain bacterial taxa, was gathered in hopes of answering three fundamental research questions: 1) Can biofilm communities unique to the SAWSs be identified using DNA analysis?; 2) Are there any taxonomic patterns that are potentially relevant to MIC?; and 3) In what ways are the site biofilms taxonomically distinct from both one another and the surrounding environment? The sampling and sequencing methodologies constitute the focus of Chapter 3, and thus, will be covered in more detail there. Sampling locations on the wreck surfaces were distributed evenly between corroded and non-corroded areas. The corresponding bacterial assemblages were compared to discern if specific taxa were correlated with the corroded surfaces. Specific attention was paid to the representation of SRB, given their documented role in promoting corrosion of submerged aluminum. Confirmation of differences in SRB or other microbial abundances could suggest that the identified microbes are either contributing to the increased corrosion, preferentially attach to corroded surfaces, or both. Regardless, a positive taxonomic association with corroded areas would warrant further investigation.

In addition to the biofilm, sediment and seawater samples were obtained from the four sites. The microbial communities yielded by these samples were also compared with the biofilms data. By doing so, the biofilm data can be assessed in terms of whether it represents genuine biofilm communities or is simply a combined product of sediment and seawater inclusion. If biofilms samples can be differentiated from those of the environment, the identification of key constituents that contribute to these differences invites speculation on the potential of niche specialization and the role these taxa play in biofilms. These ecological associations are important to consider, as it is often the synergistic activities of microbes that are responsible for triggering MIC pathways, such as oxygen concentration cells and corrosive metabolite production. By identifying the associations between microbes, it is possible to gain insights into the community composition necessary to facilitate a microenvironment conducive to MIC, while also discerning which taxa can colonize a biologically inert aluminum. Inter-site comparisons of the wreck biofilm and environmental microbiomes were also performed, with the intention of teasing out both substrate-induced similarities and geographically-related differences. The selection of sites that are comprised of essentially the same materials, located off the coasts of two different islands, further allows for inferences into which environmental factors are contributing to broader interisland trends. The entire dataset was used to determine if a MIC diagnosis could be made and which additional lines of evidence would further substantiate statements on the relevance of MIC to SAWSs.

While SAWS biofilm represents a previously unexplored microbiome, this dissertation was still guided by hypotheses informed from previous microbiological studies. The **first hypothesis** was 1) that microbial DNA extracted from samples obtained from areas of active corrosion, as indicated by visual evidence of corrosion, will indicate a relatively higher abundance of microbes linked to MIC than areas not displaying active corrosion. Specifically, SRB will be more abundant and ubiquitous among the biofilm samples from corroded locations. The **second hypothesis** was 2) that biofilm communities should reflect taxonomic associations identified in previous assessments of submerged aluminum, with aerobic microbes from the Proteobacteria and Bacteroidetes best represented. The co-occurrence of these bacteria with the previously mentioned MIC culprits may be evidence of the oxygen gradients necessary for both anaerobic metabolism and oxygen concentration cells. The **third hypothesis** was 3) that the impact of substrate material (i.e. aluminum) on shaping community composition, as inferred by comparisons with other aluminum biofilms, would be partially offset by the local environment.

Specifically, wreck biofilms should display a community composition that is in line with previous investigations of Hawaiian marine biofilms, albeit formed on non-aluminum substrates. The same is expected to be reflected by the sediment and seawater samples gathered from each site. Finally, given the responsiveness of biofilm communities to environmental conditions, the **fourth hypothesis** was 4) that SAWSs in geographical proximity (i.e. off the same island) will produce biofilm taxonomies that are more similar to one another than they are to the sites from the other island. The specific rationale, including prior studies relevant to hypotheses, are discussed in more detail in Chapter 4.

Project's Expected Significance

Underwater cultural heritage sites, even those from the contemporary past, are nonrenewable resources that are perpetually at risk of loss due to cultural and natural processes. Their protection relies on the ability of site managers to identify and mitigate these preservation threats. Yet, given the ever-increasing ability to locate UCH sites, combined with a scarcity of resources available, site management efforts must also remain cognizant of tradeoffs. While in situ preservation has long been advocated as a cost-efficient method of protection and often codified in legislation, it is no longer financially feasible to blindly commit to the in situ preservation of every site. Instead, site managers should prioritize their efforts, which shifts the conversation from what can be preserved, to what should be preserved. The latter must not only take into account academic concerns such as historical importance, but should also incorporate more socially relevant considerations related to cultural connections and economics. Additionally, preservation efforts should seek to maximize their efficacy by focusing on sites that are regularly accessed by the public. By following this approach, studies aimed at developing in situ preservation practices can enhance their overall contribution to society.

The project itself, which would be the first of its kind, can then be viewed as a justifiable effort to understand the specific threat of MIC to the in situ preservation of SAWSs. The results are the first step in discerning how microbes assemble in SAWS environments and which microbes may contribute to processes of MIC. By dealing with the issue of MIC, this project is intended to compliment the decades of research done on other preservation threats, including generalized corrosion brought upon by the marine environment, human activities (especially recreational diving), and meteorological events. Sampling efforts targeted four sites, allowing for a more in-depth assessment of the forces shaping wreck biofilm communities, including local environmental conditions. Yet, simply knowing this information on wreck microbiomes does little good on its own. The data must be critically examined in terms of its contribution to furthering the advancement of understanding MIC. Inconclusive or insufficient results should not lead to a dismissal of this project's significance, as there is an inherent value in beginning conversations about the relevance of MIC to SAWSs and providing a starting point. Both the expected results, which will become valuable legacy data for future comparative studies, and potential informational gaps can inform subsequent efforts on what has been tried and what needs to be done. In this way, the study of MIC can be an iterative process, where the approach taken in this dissertation is improved upon and refined, leading to additional insights.

The research arc started here may eventually culminate in more conclusive findings regarding the MIC of SAWSs and, even, the formulation of potential mitigation strategies. Thus, a more comprehensive understanding of the in situ preservation threats that SAWSs face should lead to more scientifically-informed management insights pertaining to SAWSs, which counter unfounded salvor claims that sites are rapidly degrading. Lastly, but no less consequential, this project is expected to contribute to the study of marine biofilms in ways that extend beyond historic preservation. The reproducible sampling protocol developed here will be shared with interested management agencies who are considering microbial impacts on SAWSs and other forms of UCH. This methodology can also be used by other researchers who seek to collect biofilm from a variety of submerged substrates, in hopes of elucidating information on the multi-faceted ecological role that these surface-attached communities play in marine environments.

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Chapter 2: The United States Navy's Trade and Exchange Program: Implications for Underwater Cultural Heritages[1]

ABSTRACT

The Secretary of the United States Navy recently issued instructions to revitalize the Navy Trade and Exchange Program, which had enabled the salvaging and collecting of sunken military aircraft in the past. Concerns regarding the program's ethics and its effect on archaeological resources led to a change in the United States Navy's policy on exchanges. Now that the program has been brought back, this paper examines its legal framework, highlights examples of shortcomings in the program's past iteration, and anticipates future outcomes in light of the program's revival. In addition to making explicit the realized and potential issues of this program, this paper encourages archaeologists to consider how recovery fits within overall site management strategies and to properly articulate to policymakers and the general public the case for in situ preservation.

Keywords: Underwater archaeology, Salvage law, Heritage management, WWII aircraft, Museum exchanges

Introduction

Beginning in the 1980s, the United States (US) Department of the Navy (DON) sponsored a system which made it possible for the DON to transfer the title of demilitarised assets in exchange for the salvaging of submerged historic naval wrecks. Known as the Navy Trade and Exchange Program (NTEP), this initiative resulted in dozens of World War II-era

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[1] This chapter is based on the article Bush (2021) "The United States Navy's Trade and Exchange Program: Implications for Underwater Cultural Heritage." *Conservation and Management of Archaeological Sites* 23(3-4): 123-144.

aircraft being raised from their watery resting places, and either designated as official DON assets or released into private collections. The ethical concerns of this practice, combined with a disregard for the aircraft as archaeological resources, led to a departmental shelving of the NTEP in 1999 (SECNAVINST 5755.2a). Twenty years later, on April 11, 2019, the Secretary of the DON issued a "complete revision" of the department's policy concerning museum exchanges (SECNAVINST 5755.2b). This action has received little formal attention from archaeologists, despite its obvious implications for underwater cultural heritage (UCH) protection and management. Though SECNAVINST 5755.2b called for a cancellation of its predecessor (SECNAVINST 5755.2a), the wording is not all that dissimilar.

The major change is a shift in attitude and intent, as evidenced by a public meeting regarding the NTEP, which took place at the National Naval Aviation Museum (NNAM) on March 12, 2019. Though it was explicitly stated to be "non-decisional" and "for fact-finding purposes only" (Naval History and Heritage Command 2019), one of the meeting's attendees stated that it was far from being an "open dialogue on the trade and exchange of Navy surplus" (H. Whitehead, personal communication, January 7, 2022). The meeting minutes revealed a strong presence of commercial salvors, including presentations on how the recovery of submerged aircraft would be incorporated into a revitalised NTEP (NNAM 2019). Additionally, the Director of the Naval History and Heritage Command (NHHC) voiced his "intent to move forward with the trade/exchange program," while the Director of the NNAM reiterated this sentiment when he committed the museum to accepting proposals under the NTEP (NNAM 2019).

In response to the DON's decision to reinstitute the NTEP, the Society for Historical Archaeology (SHA) submitted a letter to the Director of the NHHC on February 27, 2020.

Within it, the SHA (2020) expressed "major concerns about the policy" and its implications for over 15,000 aircraft wrecks under the NHHC's jurisdiction (Atcheson 2022). While the apprehension espoused by the SHA may be warranted, it is important to: (1) outline the legal framework that has enabled the NTEP, (2) understand how aircraft recovery and exchanges would work under this program, and (3) explore the possible implications such efforts would have on UCH management. By doing so, it may be possible to avoid rhetoric that places in situ preservation as diametrically opposed to recovery, while simultaneously building a coherent case against aspects of the NTEP deemed unsavoury by archaeologists. Although this discussion will be mainly limited to World War II (WWII) aircraft and policies applicable in the US, the issue of recovery and museum exchanges is all too familiar to UCH site managers around the world. Thus, this paper's intent is to encourage further dialogue among the global archaeological community as it pertains to stances on in situ preservation and recovery.

Navy Trade and Exchange Program

The origins of the NTEP can be traced to the previous director of the NNAM, Robert Rasmussen, who took over the helm of the museum in 1987 (Neyland 2002:770). Though funds for recovering downed historic aircraft were non-existent at that time, Rasmussen longed to expand the museum's WWII collection. In pursuit of this goal, he turned to an obscure section of the US Code of Laws (USC) (2010). Listed as 10 USC § 2572, the statute lays out the process for which "documents, historical artifacts, and condemned or obsolete combat materiel" can be loaned, gifted, or exchanged. The legal justification is vested within the 'Property Clause' of the US Constitution (Article IV, Section 3, Clause 2), which grants Congress the power to "dispose of and make all needful Rules and Regulations respecting…Property belonging to the United States." Materials purchased by the government during WWII for the US war effort, including aircraft, constitute ‘Property belonging to the United States’. As such, title or ownership of this ‘Property’ remains with Congress, which can delegate authority to dispose of such war materials to a federal agency.[2] In fact, for war materials, Congress has delegated authority for exchanging, gifting, and other related actions to the military branch (e.g. US Department of Army, Navy, etc.) for whom the material was purchased. Thus, while the DON does not own or have title to the aircraft wrecks or other government property, it reserves the right to make decisions regarding their use.

In 1988, the late Earl Hutto, then a member of the US House of Representatives, grew sympathetic to Rasmussen’s cause and introduced legislation amending 10 USC § 2572. The changes occasioned by the amendment included inserting the phrase “search, salvage, and restoration services which directly benefit the historical collection of the armed forces” as acceptable currencies of exchange (US Public Law 101-510 104 STAT. 1531). The NNAM’s leadership reacted swiftly, issuing a mandate encouraging the use of the newly implemented legal mechanism to acquire historic aircraft (Lyssenko 2019a:35). Enlisting the services of A&T Recovery (A&T), the NNAM first obtained a Vought SB2U Vindicator raised from Lake Michigan in 1990. A&T would go on to become the primary salvaging company relied upon by the NNAM, participating in dozens of recoveries and becoming a central figure in the debate around the NTEP. In 1992, the Secretary of the DON issued SECNAVINST 5755.1a, which provided the DON’s official guidelines regarding museum exchanges and defined the scope of the NTEP. Eventually, misgivings regarding the NTEP’s effect on naval UCH led to a

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[2] Absent proper Congressional delegation of authority, such as by a federal statute, a federal agency cannot abdicate US ownership of US war materials. For example, in Hatteras, Inc. v. USS Hatteras, 1984 AMC 1094 (1981), aff’d without opinion 698 F.2d 1215 (5th Cir. 1983), the wreck of the USS Hatteras had lain untouched since the Civil War and had been declared abandoned by Secretary of the Navy. However, salvors had no salvage rights because the US retained title and ownership of the wreck since the Navy did not have Congressional authorization to disavow ownership.

moratorium on trade proposals in 1996, and in 1999, the Secretary of the DON issued SECNAVINST 5755.2a, which effectively shelved the NTEP. The program remained dormant until 2008, when Jay DeLoach, then Director of the NHHC, expressed an interest in working with A&T to continue salvaging aircraft from Lake Michigan (Lyssenko 2019a, 96). This resulted in the recovery of SBD Dauntless (Bureau Number) 36291 (April 2009), SBD Dauntless 2173 (July 2009), F6F Hellcat 25910 (November 2009), F4U Corsair 02465 (November 2010), and FM-2 Wildcat 57039 (December 2012). In 2012, a change in the NHHC's leadership quelled support for the NTEP, until the current efforts to revitalise the program.

The original iteration of the NTEP dealt mainly with the exchange of services for demilitarised combat materiel. Using the example of A&T, the company would first agree to salvage an aircraft at the DON's request. The cost of the services rendered would then be expressed as a dollar amount, which determined the assets that the DON would sign over. A&T was then free to either hold onto said assets or convert them to cash on the open market via a commercial aircraft retailer (e.g. Courtesy Aircraft, Inc.). Some of A&T's earliest salvaging projects saw the company acquire titles to two F4F Wildcats and an SBD Dauntless (Lyssenko 2019a). A more recent conceptualization of the NTEP has shifted the burden of liquidating the exchanged naval assets from the salvor to a museum foundation (e.g. Naval Aviation Museum Foundation, Inc.). Under this structure, the DON donates the assets to the foundation, who then sells them, and passes along the funds to the salvaging company. In some cases, private donations are made either directly to the Naval Aviation Museum Foundation, Inc., or to a museum foundation of choice, in lieu of the transfer of DON assets. The foundation then oversees the contracting for all activities related to the recovery and trade of the aircraft. The salvaged plane is often given to a museum by the DON as a long-term loan.

The involvement of a foundation is not explicitly required by 10 USC § 2572. An example of an exchange under this format was presented at the 2019 Public Meeting (NNAM 2019). A&T had recovered an SBD Dauntless and FM-2 Wildcat from Lake Michigan on behalf of the NNAM in the early 1990s. With the museum unable to afford the restoration costs, both aircraft sat in storage for over 25 years. Eventually, Jerry Yagen, founder of the Military Aviation Museum (MAM), offered to pay for the restoration of the Wildcat in exchange for the title to the Dauntless. He sought to engage in a full, airworthy restoration of the Dauntless, which started in March 2021, following the aircraft's month-long public display at the MAM (Parker 2021). Yagen appraised the Dauntless wreck to be worth $150,000, which went into escrow and remained accessible to the restoration facility, the Air Zoo Aerospace & Science Museum (Air Zoo). While drawing on these funds to restore the Wildcat, Air Zoo was contractually obligated to provide Yagen with regular reports on the restoration's progress. According to Air Zoo's website, the DON retained title to the Wildcat, earmarking the aircraft for permanent display at the NNAM. In 2013, Yagen admitted to having financial difficulties, resulting in his sale of several planes to keep the MAM afloat (*Virginian-Pilot*, June 24, 2013, June 30, 2013). Though the recovered Dauntless was not among the aircraft sold, it is not difficult to see how this system can lead to situations where salvaged WWII aircraft are ultimately auctioned off to the highest bidder.

Predictably, the DON's decision to revitalise the NTEP has been received with great excitement from a particular class of aviation enthusiasts, known as 'warbirders'. Fuller and Quig (2011:275) define a warbirder as someone who is "interested in the crash sites as a source of parts for rebuilding antique aircraft." According to an online article posted by Warbird Digest on April 25, 2019, the warbirder community heralded the return of the NTEP as an opportunity for the "the recovery and release of historic US Navy or Marine Corps aircraft to private citizens, museums and/or other entities." Warbirders maintain a strong presence on the internet, through forums and blog sites dedicated to the restoration and exchange of WWII aircraft. These webpages often operate as a virtual market, where commenters can advertise or request specific parts. Additionally, many warbirders use their digital presence to document progress on their personal restoration projects. A deeper look, however, reveals that many in this community use the internet as a sounding board for complaints against those they perceive as interfering with their goals. Their ire is often focused on archaeologists tasked with the management of submerged WWII aircraft (e.g. NHHC's Underwater Archaeology Branch) (TravelforAircraft 2020a). Critiqued as being "subversive" and overly "bureaucratic," archaeologists are portrayed as hindering, rather than supporting, historic preservation (TravelforAircraft 2020b). In the US, warbirders will highlight the NNAM as an ally of their cause, pitting the museum against the NHHC and its Underwater Archaeology Branch (UAB), in a de facto battle of government versus "the American public" (Lyssenko 2019b). Framing the debate around recovery in this manner underscores the internal conflict that stems from the DON's 2006 decision to place the NNAM under the NHHC's administrative control.

Management of Submerged WWII Aircraft in the United States

In the 1980s and early 1990s, the "particular fascination of the 'warbirds' of the Second World War era" fueled a growing industry around the salvaging of aircraft crash sites (Catsambis 2012; Cooper 1994:135). In response to this exploitation, the DON shifted management responsibilities of US Naval aircraft wrecks from its Naval Air Systems Command to the NHHC (then known as the Naval Historical Center). The change in custodial duties was followed by the DON's sponsorship of a "three-year cooperative program to address the needs of aviation preservation and archaeology within the Navy" through the Department of Defense's (DOD) Legacy Program (Foster 1993:6). While the US government's interest in preserving its naval aviation history increased, so did the issue of illicit salvage operations, spurred by the demand of warbirders (Dudley 1995). This problem was exacerbated by certain aviation museums, whose lust for larger collections superseded ethical recovery and conservation practices. Those familiar with the Quonset Air Museum's failure to notify the NHHC regarding the recovery of an F6F Hellcat recovered off Martha's Vineyard in 1993 can attest to this point (Neyland and Grant 1999:47).

Recoveries of submerged WWII aircraft continued throughout the 1990s, with some permitted through the NTEP and others conducted without the necessary permissions (Coble 2001; Neyland 2002). For the latter, the DON consistently succeeded in court, thus retaining ownership over the recovered aircraft (e.g. Historic Aircraft Preservation Inc. v. One wrecked and Abandoned F4-F-4 Wildcat Fighter Airplane, US District Court, Western District of Washington at Seattle, Civil No. C95-0795 (1996); International Aircraft Recovery, L.L.C. v. United States of America, 218 F.3d 1255 (11th Cir. 2000), cert. denied, 531 US 1144 (2001)) as the US government's claim to right, title, and ownership, as established by the Property Clause, could not be usurped by unauthorized salvors, as established by the Hatteras decision noted above. In the specific case of one Curtis Helldiver, however, the judge did however, rule that the Navy's actions, including the stripping, repeated burning, and disposal of the aircraft constituted formal abandonment and awarded the wreck to the salvors (United States of America v. Jeffrey Kenneth Hummel and Matthew W Mc Cauley, US District Court, Western District of Washington at Seattle, Case No. C84-1058C).

The legal contests forced the NHHC to recognize the need to better manage the submerged wrecks under its jurisdiction, leading to the establishment of its UAB in 1996. The National Historic Preservation Act (NHPA) (1966), which “set forth the responsibility for each agency to preserve and manage historic properties under its respective jurisdiction and control” (DOD 2015a) provided the legal underpinning for the NHHC’s decision to task the newly created UAB with managing the DON’s submerged cultural resources. The UAB’s goal was to maintain an organized database of naval wrecks and ensure an archaeological approach to the management of these sites (Coble 2002). In 1999, the DON complimented its establishment of the UAB with its decision (SECNAVINST 5755.2a) to halt the acceptance of proposals under the NTEP, due to the aforementioned concerns that the program fostered an environment of exploitation (Neyland 2002). By his own admission, the current NHHC Director acknowledged that there had been “issues with the execution of the [NTEP] in the past” (Gabriel 2019).

Five years later, submerged military vessels received further protection with the passing of the Sunken Military Craft Act (SMCA) of 2004 (10 USC §§ 113 et seq). The law reaffirmed the following:

> Right, title, and interest of the United States in and to any United States sunken military craft—(1) shall not be extinguished except by an express divestiture of title by the United States; and (2) shall not be extinguished by the passage of time, regardless of when the sunken military craft sank.

Furthermore, the SCMA makes it explicit that the ‘Law of Finds’ and the ‘Law of Salvage’ do not apply to “any United States sunken military craft, wherever located…[and] any foreign sunken military craft located in United States waters”. This legislation also prohibits any physical disturbance to sunken military craft within the US contiguous zone, unless permitted through the express written consent of the permitting agency. This includes regulatory control over activities directed towards foreign flagged military craft pursuant to international maritime law, specifically Articles 95 and 96 of the 1982 United Nations Law of the Sea Convention, which recognize the precedent of warship immunity (for a more robust discussion on the SMCA, see Bederman 2006). Section 1406(b) of the SMCA states the act shall be in accordance with "international law…to which the United States is a party," subjecting any recovery of US sunken military craft within the contiguous zone, territorial sea, or inland waters of a foreign nation to regulation by that foreign nation.

By authority of the SMCA, the DOD (2015a:52588) "establish[ed] a single permitting process for persons wishing to engage in activities that disturb, remove, or injure DON sunken military craft." Under these enforceable guidelines, the NHHC's UAB receives all permit applications from individuals seeking to "engage in an activity otherwise prohibited by section 1402 of the SMCA with respect to a historic sunken military craft." The referenced section, however, also makes explicit that sunken military craft may be loaned "in accordance with regulations issued by the Secretary concerned." Importantly, the SMCA does not override 10 USC § 2572, thus allowing the DON to not only loan, but exchange sunken military craft for goods and services pursuant to 10 USC § 2572. This arrangement potentially places the UAB in an uncomfortable position, as the DON may pressure the approval of recovery permits to facilitate NTEP transactions.

Interestingly, the US Air Force (USAF) has opted for a much different approach due to a fire that destroyed "pertinent Air Force records" for crashes prior to November 19, 1961 (USAF 1994:104). The USAF (2021:184) reaffirmed its stance, stating that it "neither maintains to, nor has property interest" in the pre-November 1961 aircraft. Instead, "authority for access to, and recovery of, these aircraft" is deferred to the crash site's landowners. In the 1990s, warbirders

unsuccessfully lobbied congressional representatives to pass legislation (i.e. the ‘Warbird Act’) that would require the DON to adopt a similar policy (Neyland and Grant 1999:49).
More recently, Taras Lyssenko, president of A&T, filed a lobbying registration to represent Courtesy Aircraft, Inc. From August 28, 2019 – September 29, 2020, Lyssenko was paid to lobby the DOD and both US Congressional houses for changes related to:

> The US Navy handling of lost World War II military assets, the return to the US of World War II US Navy aircraft, the return to flight of former World War II military aircraft, [and] seeking to have the US Navy divest interest in World War II aircraft (ProPublica 2020).

As a part of these efforts, Lyssenko (2019b) made public his “Open Letter to the Acting Secretary of the Navy and the Chief of Naval Operations,” in which he concluded that “the National Naval Aviation Museum and the American public are far better stewards of the once lost US Navy World War II aircraft” than the NHHC. The letter, however, failed to provide any concrete evidence of the NHHC’s supposed mismanagement.

Though the NTEP would satisfy requirements put forth by the SMCA, it is less clear how the program accords with the NHPA. Viewed as the principal preservation law in the US (Banks and Scott 2016; McManamon 2018), the NHPA provides legal protections for sites and places meeting the eligibility requirements (‘level of significance’) for listing on the National Register of Historic Places (NRHP). The law is often thought of in terms of its Section 106 provision, which mandates that any involvement from the federal government (i.e. permitting and/or funding) requires the agency “to take into account the effects of their undertakings on historic properties,” including those already on the NRHP and those eligible for listing. Based on the levels of significance put forth by the NRHP’s Criteria for Evaluation, WWII aircraft clearly constitute historic properties in the eyes of the law (Table 2.1). Among its critiques, the SHA (2020) letter points out that SECNAVINST 5755.2b does not mention how the recovery of wrecked aircraft, as permitted under the NTEP, will comply with the protections afforded to historic properties by the NHPA. This omission could create the proverbial 'slippery slope' as historic preservation laws, both at the federal and state-level, are bypassed by government-endorsed trade programs modelled after the NTEP. To ensure against this, the NHHC could establish a NHPA Section 106 Memoranda of Agreement (MOA) or Programmatic Agreement (PA) that would require all actions permitted under the NTEP to be consistent with the NHPA. The US Department of Housing and Urban Development (HUD) (2021) provides a database of such MOAs and PAs containing agreements from across the country for HUD-related projects, which are used to model future agreements concerning Section 106 compliance.

Table 2.1. National Historical Preservation Act Criteria

Level of Significance	**Description**	**Applicability to WWII Aircraft**
A	Associated with events that have made a significant contribution to the broad patterns of our history	Yes
B	Associated with the lives of significant persons in or past	Maybe
C	Embody the distinctive characteristics of a type, period, or method of construction, or that represent the work of a master, or that possess high artistic values, or that represent a significant and distinguishable entity whose components may lack individual distinction	Unlikely
D	Have yielded or may be likely to yield, information important in history or prehistory	Yes

Potential Issues with Navy Trade and Exchange Program

While the NTEP is designed to increase public access to historical resources and support the preservation of said resources, it is hard to overlook the financially focused rhetoric from proponents of the program. On the extreme end, Taras Lyssenko, perhaps the most vocal supporter of the NTEP from within the private sector, hypothesised that the DON could exchange up to "100 million dollars" annually in assets under the program (Gabriel 2019). The NNAM director was also keen on identifying the approximate dollar amount, 10 million, when describing the positive impact the NTEP had on the museum and its collections (Gabriel 2019). Today, vintage WWII-era aircraft regularly fetch six-figure paydays for the seller, with rarer makes and models easily exceeding $1,000,000 per aircraft. In 2020, two North American Aviation P-51 Mustangs were listed for $3.9 million and $2.5 million, respectively (Suciu 2020). With stakes such as these, historical aircraft are conceptualised in the same fashion as any other commodity traded on the open market. For historical cultural resources, this exploitative ethos has traditionally led to a disregard for an artifact's emotional significance, on both a personal and national level, in favour of profit (Brodie and Luke 2006; Burtenshaw 2014; Campbell 2013; Gerstenblith 2007). Furthermore, this profiteering is antithetical to the historic preservation ethos ascribed to by most professional site managers and codified in the US historic preservation laws (Borodkin 1995; Harmon et al. 2006; King and Lyneis 1978; Sokal 2006). Furthermore, activities directed towards cultural heritage resources that are motivated by profit would qualify as 'commercial exploitation', which is explicitly prohibited by Article II of the 2001 UNESCO *Convention on the Protection of the Underwater Cultural Heritage*. The Convention acts as an international legal codification of the professional ethics of archaeologists and museum associations, including the International Congress of Maritime Museums.

To ensure future recovery operations sanctioned under the NTEP avoid the above-stated consequences of commodification, one can look at examples of shortcomings in the NTEP's past. The first incident of note occurred in 1994, when the NNAM contracted A&T to raise SBD Dauntless 10694 from Lake Michigan (Veronico 2013:48). Though the recovery was successful, the museum lacked the necessary funds to reimburse A&T for its services. Left with little choice, the DON permitted the NNAM to allow A&T to recoup its profits by authorising the sale of the Dauntless to a private collector. Billionaire Jim Slattery purchased the aircraft and financed its airworthy restoration, before placing it within his private museum. (Hodson 2013; Roeder 2016). In this case, the NTEP created a market for the sale of a submerged WWII aircraft that otherwise would not have existed without the DON's authorization for recovery. The DOD (2011:21) echoed a similar sentiment, concluding that:

> Removing from the public historical artifacts for re-issuance to private organizations establishes a dangerous path. What would stop an individual of wealth from purchasing other items of historic value? Could the Wright Flyer be purchased for personal use/display?

Ironically, the DOD is now providing such opportunities via the NTEP.

The example of SBD Dauntless 10694 sets an uncomfortable precedent in which those with the financial means can simply purchase recovered aircraft, effectively taking it out of the public collective and allowing it to enter private hands for singular use. For many private collectors, the latter can often entail an airworthy restoration, where many of the original parts are replaced due to decades of submergence. The mass production of aircraft components during the war and the interchangeability of comparable post-war parts simultaneously enables replacement during restoration, while creating a sub-market focused on the sale of individual aircraft parts (Diebold 1993). When parts are swapped or markings painted over, the history of the plane is essentially erased and "discarded in favour of a new, more marketable, identity" (Gillespie 2011:264). No longer was the Dauntless an original representation, but instead, a highly altered version fitted with provenance-less replacement parts. Fix (2011:992) writes that this "Frankenstein fabrication process" is intended to bestow upon the aircraft a "newness value" that is otherwise lost when viewing a wrecked aircraft. The emotional trauma associated with the wrecking is masked by fresh aesthetics designed to capitalise on feelings of nostalgia rather than preserving and conveying the plane's individual history (Wayland 2006:44-45). The aircraft is no longer the machine used during WWII, but instead, a composite of original and substitution parts, which can conceal how “the pressures of combat” led to nuanced modifications (Holyoak 2001:259). In essence, such ‘restoration’ completes the destruction of the aircraft it once was. The excitement surrounding the successful recovery of a submerged aircraft wreck can lead to the logistics of restoration, and by extension, the entire conservation process, being overlooked. This ignorance further exacerbates the ‘curation crisis’ (Kersel 2015; Voss 2012), which refers to an accumulation of artifacts that results in an unsustainable surplus and the inevitable neglect or improper treatment of certain items. This problem intensifies with the complexity and scale of the collection materials, thus, making recovered aircraft among the most difficult to conserve. For planes recovered from aquatic contexts, attempts to undo the effects of corrosion often require a substantial amount of time and resources, including access to electrolytic reduction facilities and specific chemical reagents (Hamilton 1996). These issues are made considerably worse when an aircraft is recovered from a saline environment, as salt adds an extra dimension of difficulty to the conservation process (Hamilton 1999; Pearson 1987; Rocca et al. 2019).

Though warbirders remain optimistic about the possibility of recovering submerged aircraft wrecks (Veronico 2013:32), the funding, space, and personnel necessary for the requisite conservation techniques are often lacking. In a review of the NHHC, the Naval Inspector General (2011:5) concluded that there was “no comprehensive plan for facilities and operations for the 11 museums” under the NHHC’s direction. Furthermore, the Naval Inspector General found that the NHHC was then in possession of 200,000 assets requiring full time curation, with a backlog of an additional 60,000 artifacts. Issues with chain of command communication, quality of work life for personnel, and a general tendency of the NHHC to be reactionary rather than proactive led to the DON’s 2012 decision to replace then-NHHC Director and ardent supporter of the NTEP, Jay DeLoach. The Naval Inspector General’s (2011:30) report also stated that the NNAM “employed improper procedures and processes to restore vintage aircraft.” This finding was based on a review of industrial hygiene surveys for the museum, which revealed workplace contamination, personnel exposure to toxic metal dust, and the improper offloading of chemical waste. As a result, the NNAM shuttered aircraft restoration activities in 2011 for over a year. This shutdown halted the progress of conservation projects at NNAM, including that of SBD Dauntless 2173, which had been recovered from Lake Michigan by A&T in 2009. According to Air Zoo’s website, by the time the NNAM instituted the necessary compliance measures, the museum lost most of its volunteer staff, causing the price of restoration for the Dauntless to skyrocket from $300,000 to $1,200,000. For the next five years, the aircraft sat in anonymity at a storage facility in Pensacola, Florida, until the situation became untenable. In 2016, the NHHC was forced to turn to another restoration option, Air Zoo, which agreed to take on both the Dauntless project and other restorations on behalf of the NNAM. This situation exemplifies how the unpredictability of conservation work makes aircraft recoveries an especially risky endeavour. There is no guarantee that treatments plans will be followed as scheduled, which is why a projected 3-5-year restoration took 12 years to complete. Though the ending for SBD Dauntless 2173, which was sent to Pearl Harbour Aviation Museum (PHAM) as a part of the 80th Anniversary Remembrance Ceremonies for Pearl Harbour, is a successful one, this may not always be the case. All parties involved in the recovery of submerged aircraft wrecks should consider the long-term conservation plan for these non-renewable resources.

This discrepancy between conservation needs and the available funding creates further opportunities for those with the financial means to dictate the terms of the conservation process. This divergence is expected to increase with the recoveries of additional aircraft, as current means of funding are exhausted and inventories continue to backlog. Though the DOD

(2015b:69) has issued specific advice to "[a]void stockpiling condemned or obsolete combat materiel in anticipation of future exchanges," it is not hard to imagine a scenario where unchecked recoveries lead to situations in which aircraft either languish without proper conservation or only receive the requisite treatment with a strings-attached deal. This is not to say that museums and historical resource managers should not welcome the financial support of benefactors from the private sector, but rather, they need to remain cognizant of those who offer financial assistance in order to acquire historic aircraft for personal gain.

Finally, the promise of recovery is a particularly potent way of drawing interest from aviation enthusiasts, who see the activity akin to rescuing history. The dubious financial motives of this approach are evidenced by the case of The International Group for Historic Aircraft Recovery (TIGHAR) and the Douglas TBD Devastator of Jaluit Atoll (Marshall Islands). Following a DOD-sponsored site evaluation, TIGHAR (2007:3) announced the NNAM's intention of receiving the aircraft upon its recovery, writing that "four years and half a million dollars later, most of the hurdles have been cleared and recovery is now more a matter of 'when' than of 'if'." Freedom of Information Act (FOIA) records indicate that the non-profit even entered into a contract with the DON to recover the Devastator (FOIA Case No. 2010F010444). A decade passed, which saw TIGHAR aggressively pursue additional funding from its members for this endeavour, purportedly totalling $207,000. However, the project was abandoned in 2016, at around the same time the organization's leader began to field inquiries about how project funds were being spent (Fowler 2017). A scan of TIGHAR's website as of the date of this article reveals the potential for a similar occurrence regarding the recovery of the famed Maid of Harlech, a P-38 Lightning crashed off the coast of Wales. TIGHAR began advertising the possibility of recovery in 2007 with calls for donations such as this one:

> Contributions to the Maid of Harlech Memorial Fund go to help cover TIGHAR's expenses in advocating for the responsible recovery and conservation of Lockheed P-38F 41-7677. If you wish, you can make your donation of $100 or more in the name of any World War II veteran. When the aircraft is recovered, a permanent memorial with the names of the donors and honorees will accompany the P-38 to the accessioning museum.

The solicitation appears to assume recovery (despite legal protections placed on the aircraft by both the US and United Kingdom governments), while also promising permanent recognition for the donors. In the author's opinion the option of donating in the name of a WWII veteran for a project that may never come to fruition would appear at best inconsequential and at worst, emotionally manipulative.

Archaeology and the NTEP

From an archaeological perspective, one of the main issues with historic aircraft salvaging has been a reluctance to employ proper archaeological methods and collaborate with professional archaeologists. A&T states that its operations are not guided by the NHHC's Methods and Guidelines for Conducting Underwater Archaeological Fieldwork, but instead adhere to "the same methodology utilized by the Navy's Supervisor of Salvage" (Lyssenko 2019b). This presumably refers to the Chief of Naval Operations' OPNAVINST 3750.6S (and its predecessors) and the US Navy Salvage Manuals (Volumes 1-4). These instructions are explicitly intended to guide the recovery of modern military assets. These salvage-focused methodologies appear inappropriate as the SMCA bans the application of the 'Law of Salvage' on sunken military craft without the consent of the US or the foreign state in the case of foreign sunken military craft. The methodology advocated by the NHHC's guidelines, on the other hand, places a greater emphasis on research design and aircraft as historical resources. A&T's refusal to incorporate both sets of instructions represents an intentional choice to dismiss the utility of archaeological methods. When raising SBD Dauntless 2106 from Lake Michigan in 1994, the president of A&T actively fought the involvement of an archaeologist on the project, while failing to utilise the documentation template provided by the NHHC. Lyssenko (2019a:62) proudly stated that the archaeologist "was not allowed anywhere near recovery activity." Yet, there are those, such as the current NHHC Director, who believe that the NTEP will strike the "balance between lifting aircraft from their crash sites and preserving archeological fidelity" (NNAM 2019). This sentiment seems highly unlikely given the inflammatory rhetoric and deep-seated disdain for archaeologists that aircraft salvors have historically expressed.

Furthermore, it is difficult to evaluate whether salvors are capable of the proper documentation when there is a refusal to share information. According to Lyssenko (2019b), Robert Neyland, on behalf of the NHHC, inquired about information regarding known wrecks in Lake Michigan. Lyssenko claimed that the data was "intellectual property that belongs to a private company" and rebuffed Neyland's request. Lyssenko (2019b) admitted that his company had attempted to use the sharing of wreck information as a bargaining tool pertaining to recovery proposals submitted by A&T. As those discussions progressed, A&T's leadership felt that the NHHC's insistence on adhering to proper archaeological guidelines "made it impossible for A and T Recovery, L.L.C. to perform the tasks." In light of this assessment, A&T decided it would "begin sharing with the American sport diving community locations of the remaining once lost US Navy World War II aircraft of Lake Michigan," couching it as "*pro bono publico*." It is apparently only after A&T rejected the NHHC's stipulations that Lyssenko felt it necessary to act 'for the public benefit'.

This lack of transparency is most worrisome given the issues of missing servicemembers. Without the appropriate oversight, human remains or key identifiers of specific aircraft may be overlooked during non-archaeological salvage projects, resulting in lost opportunities to bring about closure for grieving families. Such may have been the case with SBD Dauntless 1612, whose pilot, Ensign Herbert W. McMinn, was killed during a training incident over Lake Michigan (*Chicago Tribune*, November 23, 1942). Though neither his body nor parachute were ever recovered, McMinn's Dauntless was raised from the water in 1994 by A&T, and according to Air Zoo's website, put on display at the Flying Leatherneck Aviation Museum (FLAM). While it is unclear what may have been found had the salvors collaborated with archaeologists, the decision to recover the aircraft is fraught with concerns. On a personal level, neither the NNAM nor A&T extended notified Ensign McMinn's family about the recovery in 1994. It is only during his preparation for speaking at the FLAM's gala in 2017 that A&T's president finally reached out to Ensign McMinn's great-grandson (Lyssenko 2019a:155-156). This disturbance of a war grave and the initial disregard for the familial element exemplifies the ethical issues inherent in reducing these aircraft to commodities and items of salvage.

Internationally, a similar situation has arisen in Papua New Guinea (PNG), which serves as a rich repository for downed WWII aircraft. Due to a lack of governmental oversight, PNG's WWII cultural heritage remains under constant siege by collectors and salvors. As a result, the US government, which "invests hundreds of millions of dollars to recover the remains of World War II pilots" from crash sites, constantly finds itself "in a race against relic hunters" (Baron and Bender 2009). The hunters' lack of proper archaeological fieldwork, combined with their prioritization of profit, has inevitably led to a situation in PNG, where "by the time recovery teams arrive at suspected MIA sites, the locations often have been picked over and crucial evidence is missing" (Baron and Bender 2009).

The focus thus far on submerged wrecks is largely born out of the fact that many terrestrial crash sites were salvaged in the decades that immediately followed WWII, when aircraft were not yet considered historical resources (Fix 2011). While Lake Michigan has proven to be a source of potential recoveries, few inland bodies of water saw a significant amount of aviation wreckage. Thus, as Ric Gillespie (2011:270), Executive Director of TIGHAR, wrote:

> After 40 years of scouring the mountains, lakes, and jungles for salvageable vintage wrecks the cupboard has become relatively bare… For new accessions of genuine historic aircraft, museums are being forced to turn to the world's oceans and bays that still hold many significant wrecks.

The NHHC's support of the NTEP could make this shift towards marine recoveries an even greater probability. This expands the current archaeological relevance of the NTEP from beyond the Great Lakes, and to the world's oceans. An estimated 40% of historic US naval wrecks are found in waters beyond the US Exclusive Economic Zone (Atcheson 2022). The principle of sovereign warship immunity, as codified by the SCMA and International Maritime Law, means that these sovereign or public vessels in foreign seas are immune from arrest and remain property of the US unless expressly abandoned. They may be eligible for recovery under the NTEP if, as noted before, authorised by the foreign state which has regulatory authority and jurisdiction over them within the foreign contiguous zone and with the required consent of the US.

In the Asia-Pacific area, where war was waged primarily by naval and aerial forces, submerged aircraft wreck sites often serve as popular diving destinations. This is not to reduce the significance of these planes to tourism data, but instead, their attraction is directly owed to their cultural importance (Edney et al. 2021). The ability of submerged historic aircraft to act as 'diver aggregation devices' (Edney 2017:169) is largely owed to their historical originality and national attitudes towards military history. Additionally, divers appear to be drawn specifically to aircraft wrecks due to the novelty of seeing a machine intended for flight underwater and the smaller scale that enables a more personal experience (Edney and Boyd 2020).

The demand for site access by divers has led to significant economic opportunities for boat charters, dive guides, and other businesses directly serving the scuba tourism industry (Musa and Dimmock 2013). In turn, this type of non-consumptive site interaction (Kaoru and Hoagland 1994) supports the hospitality sector, which remains a crucial component of local island economies who often lack exportable goods (McElroy 2003). Though contemporary aircraft can be scuttled for diving purposes, these planes lack the historical context that often serves as a strong motivation for visitation (Edney and Spennemann 2014, 2015). Additionally, if WWII aircraft are removed from their marine locales, it is unlikely they will be returned post-conservation to local museums on-island. Instead, US mainland institutions, such as the NNAM, will be the probable beneficiaries of recovery missions. On Balalae (Solomon Islands), for example, dozens of WWII aircraft have already been recovered by foreigners who have found loopholes within the Solomon Islands' Protection of Wrecks and War Relics Act (1980). The potential lack of compensation, combined with the planes' historical significance, has led some Solomon Islanders to express "concern over their removal, arguing not only that this affected future tourist potential, but also that it meant the removal of part of the history of the province and its people" (Forrest and Corrin 2013:5). In 2018, this trend continued when two non-US WWII aircraft (Mitsubishi G4M) were prepared for removal from Balalae under the guise of a non-enforceable MOA (Ragaruma 2018).

Discussion: When to Recover

A common charge against archaeologists is that their advocacy for in situ preservation is synonymous with a rigid opposition to all recovery projects, which frequently does not sit well in court of public opinion (*Virginian-Pilot*, August 23, 2004). The latter was palpable in a webinar on underwater aircraft archaeology hosted by PHAM that featured the author. Despite the focus of the event being on how archaeologists utilise various scientific approaches for the in situ preservation of submerged aircraft wreck sites, the top question posed by the audience pertained to the issue of recovery. Given this innate interest in recovery, the onus should be on professional archaeologists to adequately articulate the rationale for choosing in situ preservation, especially in light of a national program aimed at incentivising the alternative.

The Annex to the 2001 UNESCO *Convention on the Protection of the Underwater Cultural Heritage*, which remains the guiding principle for underwater archaeologists (González et al. 2009), has codified this fondness for in situ preservation by listing it as the “first option” (or ‘preferred’ option, depending on the translation) (Aznar 2018). It should be noted that UCH, as defined by the 2001 Convention, includes heritage resources that have been submerged for at least 100 years, the same threshold for archaeological resources under the US Archaeological Resources Protection Act (1979). Thus, sunken WWII-era vessels are still 17-23 years from that threshold (at the time of printing). While the US has yet to ratify the Convention, 71 (and counting) state parties have, which will eventually provide significant international protections to WWII wreck sites in those countries’ waters. As such, salvors, either authorised by the DON or beyond the reach of the SMCA’s jurisdiction, may see this interim period as a time to make a concerted effort to recover US vessels in foreign waters before the 100-year threshold activates those safeguards. Thus, there is presently a greater need for ensuring that recoveries and exchanges authorised by the DON under the NTEP are consistent with legal protections put forth by the NHPA, and hence, the importance of establishing Section 106 compliance MOAs or PAs as referenced above.

The preference for in situ preservation is born from a non-consumptive philosophy and “based on the recognition of the importance of the interplay between the site, its story and its context” (Maarleveld et al. 2013:20). Preserving this ‘importance’ for current and future stakeholders, however, does not permit archaeologists to remain inactive or passive as it pertains to site management. Instead, in situ preservation should be approached in a comprehensive manner that involves all “steps taken on a site or intervention with a site in order to extend its longevity while maintaining original context and spatial position” (Ortmann et al. 2010:28). This definition encompasses a broad range of actions, including documentation, photographing, three dimensional (3D) modelmaking, monitoring (e.g. corrosion or visual) surveys, and interventive means of site protection (e.g. reburial).

The holistic conceptualization of in situ preservation negates the misnomer that archaeologists condone the unchecked corrosion of UCH. This accusation is frequently levied, as expressed by Lyssenko (2019b), when he stated his belief that the NHHC “are allowing many historic aircraft to corrode to nothing … when they could be recovered and presented to the public.” A similar sentiment was voiced at the 2019 public meeting on the NTEP, when a marine salvage lawyer said of archaeologists, “Their opinion is to leave it where it is because it is preserved. However, [the wrecks] are deteriorating.” Statements such as these ignore the science-based assessments of marine archaeologists, who employ rigorous analytical techniques to discern UCH decay trajectories. For underwater aircraft wrecks, understanding the site transformation processes initiated by the plane’s submergence requires an interdisciplinary approach. Research on the in situ corrosion of submerged WWII aircraft in Chuuk (MacLeod 2006) and Saipan (Richards and Carpenter 2012, 2018) revealed that subtle variations in a wreck’s exposure to dissolved oxygen can lead to significant differences in the frequency of corrosive redox reactions. Similarly, the composite makeup of an aircraft, consisting of different metals and varying degrees of electrical connectivity between individual components, can also lead to higher or lower levels of corrosion. Recently, the effect of corrosion brought on by the metabolic activities of colonising microorganisms has become a topic of interest concerning shipwreck sites (e.g. Hamdan et al. 2021; Lee and Little 2019; Mugge et al. 2019; Price et al. 2021), and is already being studied within the context of submerged aircraft sites off the coast of Hawaiʻi (Bush et al. 2021).

Corrosion studies, both biological and electrochemical, enable site managers to gain empirical data that aides with determining if and when recovery is necessary. These results can be presented to the public and government officials, in an effort to combat the unfounded claims of imminent destruction used to justify recovery. Identifying changes in a site's corrosion parameters may also provide resource managers with ample time to implement various mitigation measures (e.g. sacrificial anodes, reburial, or relocation) (Manders et al. 2008). Additionally, investing in this sort of site management may aide with future recovery projects, as it bides time for funding acquisition, fostering institutional support for salvaged aircraft collections, and developing better recovery and conservation technologies. An improved understanding of preservation threats eliminates the temptation for rushed recovery operations and allows for a more feasible recovery. After 80 years of being submerged, the idea that these aircraft are now suddenly on the verge of complete destruction may be overstated.

In situ preservation should also seek to enhance site interpretation, which has led to a rise in the establishment of 'heritage trails' that are accessible to divers and snorkelers. No longer are wrecks viewed as disconnected occurrences on the seafloor, but instead, these trails help to better contextualise individual sites within the broader maritime cultural landscape (Philippou and Staniforth 2003). Replete with dive guides and on-site descriptive plaques, this form of site management has increasingly been recognised as a way of fostering an appreciation for UCH that does not require recovery (Leshikar-Denton and Scott-Ireton 2007; McKinnon 2013; Scott-Ireton 2005; Scott-Ireton and McKinnon 2015). Success of these 'underwater museums' will be key in changing the societal perception of aircraft from salvageable resources to sites deserving of reverence akin to national landmarks.

As an additional alternative to recovery, the incorporation of 3D photogrammetry and immersive virtual reality has allowed site managers to aesthetically present wrecks to the public without removing a single aircraft part from its submerged location. These innovative forms of technology, which do not require the large capital needed for recovery and conservation, are already being applied within the field of maritime archaeology (Bruno et al. 2019; Doležal et al. 2019; Liarokapis et al. 2017). This approach allows wrecks that currently serve or have the potential to serve as popular diving destinations to remain in place and accessible to local communities, while the 3D depictions are made globally available (Čejka et al. 2020). These models present the sites to non-divers much like a museum would, but within the context of their original historical position. This approach serves as an alternative to heritage trails and underwater museums that require users to possess the capital necessary to travel and dive on a site. It is this spirit that Heritage Malta launched its virtual underwater museum in 2020, which showcased nine WWII aircraft among other submerged wrecks. Rendered in stunning detail, Blue (2021:1347) described the exhibition as:

> It will not only be of interest to maritime archaeologists and historians, but will also be enjoyed by those attracted to the regional history of Malta, 3D modelling and, importantly, viewers interested in the exciting new world of virtual museum exhibitions, something we will no doubt see more of in the future.

Exhibiting submerged aircraft wreck sites in this fashion allows users, without any direct costs, to visualise an airplane within its aquatic context, while potentially presenting some of the unique diver motivations associated with this site category to non-divers.

When recovery is considered, decisions to do so should take into account the socioeconomic significance a site may have. As mentioned earlier, the diving and snorkelling industry is a prime example of how an initiative such as the NTEP may create unneeded conflict through consumptive site use (Kaoru and Hoagland 1994). Complete or nearly complete aircraft are the most desirable for recovery, as it means less reproduction and substitution parts. However, these planes are also the most sought after by recreational divers. The SB2C Helldiver off Maui, the Aichi E13A in Palau, and the P47 Thunderbolt off Raja Ampat, Indonesia come to mind as just a few examples of popular aircraft dives. In an interview with LiveScience on February 21, 2020, Colin Colbourn of Project Recover, postulated that "[a]irplanes [in Chuuk] that broke into fragments aren't necessarily recognizable to recreational divers," and thus, have been overlooked for decades. A site's recognisability as an aircraft is a primary factor in satisfying the motivations that draw visitors to a wreck (MacLeod and Harvey 2014). This puts those that seek to recover at odds with those who depend on access to complete, or nearly complete, submerged aircraft. With A&T's president stating that "there are always aircraft we should recover" (Lyssenko 2019a:133), it is necessary to be explicit about which aircraft should be deemed candidates for recovery from a management perspective.

Along with significance, a site's accessibility should constitute an important factor in the decision to recover. Wrecks that are easily accessible and regularly visited are often incorporated into an area's cultural landscape and heritage tourism industry. Conversely, aircraft left in logistically difficult places to reach are often devoid of much human interaction, and may fall victim to being 'out-of-sight-out-of-mind' (Gregory 2009). Wrecks under this designation could serve as possible candidates for recovery, given the demand for it. The aforementioned SBD Dauntless 2106, in whose recovery A&T refused to allow NHHC archaeologists to participate, serves as an example of where recovery is not only permissible, but, perhaps, preferable (Lyssenko 2019a:62). A survivor of the attack on Pearl Harbour and a participant in the Battle of Midway, the aircraft was lost in 1942 during carrier operations training in Lake Michigan (Wills 1997). Resting nearly 50 metres below the surface, SBD Dauntless 2106 was only relocated as a part of a survey conducted by A&T on behalf of the NNAM. Its location within the muddy, dark depths of Lake Michigan was not considered conducive to public access. Today, it is the only known survivor of Midway on display.

For SBD Dauntless 2106 and many of the aircraft retrieved from Lake Michigan by A&T, the decision to recover is not necessarily objectionable, but rather, the execution of such recoveries raises legitimate concerns. Archaeological oversight within a recovery operation is meant to serve the public's best interest, as the training and expertise of the archaeologist can help preserve aspects of a site's history that otherwise would have gone unnoticed. Additionally, a salvage operator's general dismissal of professional archaeologists and proper archaeological documentation undercuts the idea of recovery as an acceptable resource management strategy. As Cooper (1994:135) stated, "[b]ereft of archaeological mitigation or cultural resource management considerations, these salvage operations have helped legitimise and encourage aircraft salvage operators, fostering a public salvage mentality regarding historic aircraft wrecks." As access to the technologies that enable site location increase (Browne 2019), so will illicit recoveries of historic aircraft that are simply viewed as commodities by a program that encourages recovery. Collaborations between archaeologists and those working in the salvaging and museum fields could help to dispel this idea that recovery is divorced from research and management.

Finally, restoration need not be the only end goal of recovery for aircraft intended for museum use. The NNAM has an "Underwater Treasures of Lake Michigan" exhibit featuring wrecked aircraft in simulated aquatic environments, while the strewn wreckage of a Mitsubishi A6M2 from the famed Niihau Incident is on display at the PHAM. In both instances, public access to the crash sites is either limited or non-existent, making a museum display a particularly relevant way of presenting the individual histories of these aircraft. Similarly, the Dutch Military Aviation Museum offers visitors the chance to view conserved WWII aircraft wreckage adjacent to full-scale replicas (Gillespie 2011:270). This form of exhibition confronts the viewer with the carnage of war, while providing a recognizable prototype that satisfies feelings of nostalgia. As WWII slips further from the present, the idea that aircraft associated with this global conflict must either be left alone or recovered and restored to their 'full glory', should be replaced by more nuanced approaches to site management.

Conclusion

Military aviation history tends to be memorialised through its machines, given the difficulty in preserving an ephemeral aerial battlefield (Kohn 1995). As such, aircraft have become lightning rods in the discussion surrounding how to best proceed with historical preservation, leading some to argue for wreck recovery. This desire to salvage WWII naval aircraft, which served as the original impetus for the NTEP, ultimately influenced the DON's recent decision to revitalise the program. This action has placed additional conservation and management considerations for a site category (i.e. WWII aircraft crash sites) that is already prone to illegal salvaging. The NTEP's history is rife with examples of exploitative attitudes and disregard for the public collective, which should foster a healthy scepticism about the future execution of the program. Yet, there exists potential for situational compromises that balance public access and historical preservation with the goals of the NTEP. Archaeologists and site managers tasked with helping to strike this balance should refrain from engaging in an ideological battle between uniformly accepting or rejecting recovery as an option. Rather, archaeologists should be prepared to present compelling and explicit cases, if one can be made, for why a submerged aircraft should be preserved in situ. For example, in situ preservation should remain the preferred style of management for aircraft that are regularly relied upon as diving tourism sites, or when the cultural context of a site (e.g. as a war grave), dictates that it should not be disturbed. This, however, does not mean in situ preservation must remain strictly passive, but rather, requires that resource managers monitor and document wreck sites so that informed decisions can be made.

The future impacts of the NTEP will likely be most relevant to sites located within the world's oceans, especially the Pacific. After nearly eight decades of scavenging terrestrial and lacustrine wrecks, the ocean will be the final frontier for the relocation of WWII aircraft. Those who wish to recover aircraft, may do so out of genuine concern for the well-being of the general public and status of the wreck. However, it is easy to recall past scenarios and imagine future ones where recovery is motivated by money and self-interest. Even with the best of intentions, decisions regarding recovery must be informed by science and planned with a proper understanding of the resources necessary for proper conservation. When issues of funding, facilities, and labour are ignored, it becomes possible for detrimental interruptions in the conservation process, which can irreversibly harm the physical status of a wreck.

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Chapter 3: In Situ Biofilm Collection and the Management of Historic Submerged Aircraft Wreck Sites[1]

ABSTRACT

The impact of microbiologically-influenced corrosion on underwater archaeological sites has spurred recent advancements in research examining the link between microorganisms and historic preservation. The shifts in ocean conditions associated with climate change will undoubtedly affect the microbial communities that colonize submerged cultural resources, with uncertain consequences for site preservation. While the microbiomes of steel shipwrecks sites have been the subject of DNA sequencing studies and other interdisciplinary investigations, aluminum submerged aircraft wreck sites, a prominent symbol of World War II, has yet to be the focus of similar research pursuits. This article represents the initial step to confront this void by describing a biofilm collection method used to obtain samples for DNA sequencing from World War II aircraft sites off Hawai'i. Rather than relying on proxies for microbial growth on wrecks, or destructive sampling, the focus is on a methodology that is productive, yet minimally-intrusive. The protocols put forth are intended to be affordable, time-efficient, and reproducible, thus being feasible for archaeological site management. The development of viable, in situ collection methods for biofilm will aid efforts to empirically assess the relevancy of microbiologically-influenced corrosion to submerged aircraft, while also enabling longitudinal studies of microorganisms that potentially impact site preservation.

Key Words: Aircraft, Microbiologically-Influenced Corrosion, World War II, Biofilm

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Introduction

Within maritime archaeology and cultural resource management, an increasing amount of attention has been paid to discerning the impacts that climate change has on underwater historical sites that are deemed to be ‘heritage at risk’ (Miller and Wright 2023). Rather than being resigned to reactive responses to climate-induced damage, heritage professionals have recognized the value in proactive approaches that seek to anticipate future preservation threats. There exists a growing body of knowledge pertaining to the ways in which shifting ocean conditions associated with climate change are expected to facilitate detrimental site transformations (Fernández-Montblanc et al. 2022; Hafner et al. 2020; Perez-Alvaro 2016; Underwood 2022; Wright 2016). Gregory et al. (2022) highlighted specific examples regarding seabed erosion, temperature, elevated carbon dioxide, and dissolved oxygen. Integration of interdisciplinary methods and communication about these research experiences have been key in supporting these efforts. The iterative process of studies that examine the link between climate and underwater cultural heritage (UCH) building, refining, and improving upon each other has led to numerous insights. Nevertheless, the sheer pervasiveness of climate change impacts on the ocean, ranging from warmer temperatures to increased acidification and extreme weather events, has inevitably led to informational gaps. This is especially true about the predicted role of the microorganisms that colonize submerged archaeological sites.

The connection between microbes, climate change, and heritage preservation is admittedly not an obvious one. The linkage is made apparent, however, when considering the effects microbiologically-influenced corrosion (MIC) has on metallic UCH. Nested within the burgeoning field of ‘wreck ecology’, MIC studies have taken aim at assessing the damage inflicted upon heritage resources, identifying the associated microbes, and elucidating information on MIC mechanisms (Paxton et al. 2024). This has often been achieved through collaboration and the utilization of analytical techniques from outside traditional archaeological practices, namely next-generation DNA sequencing. Using both the collection of on-site samples and mesocosm experiments, the results paint a complex picture of ways in which microorganisms contribute to corrosion. While this data is immensely informative for the current understanding of MIC and UCH, research from beyond archaeology suggests that the ocean's microbiota is unlikely to stay static.

Studies of free-floating, sedimentary, and surface-attached (e.g. biofilm) communities have highlighted a myriad of examples in which these microbial assemblages are impacted by many of the same climate change variables described by Gregory et al. (2022) (Abirami et al. 2021; Arromrak et al. 2022; Baltar et al. 2019; Caruso and Ziervogel 2022; Coelho et al. 2013; Collins et al. 2020; Ducklow et al. 2010; Hutchins and Fu 2017). Whether these changes, both taxonomically and functionally (i.e. gene expression), will correlate with an increase of MIC-related damage to UCH remains largely unexplored (Melchers 2014). Resolving this ambiguity requires that heritage managers have access to both baseline observations of microorganism populations and comparative datasets. By doing so, alterations in the microbial communities can be longitudinally tracked with changes to a site's physical status and seawater conditions (e.g. temperature, pH, and dissolved oxygen). This places a premium on the development of sound microbiological collection techniques.

Much of the MIC pursuits in maritime archaeology have been devoted to steel shipwreck sites, with dissemination of this research not only providing site-specific data, but also resulting in the exchange of methodologies (Albahri et al. 2019; Church et al. 2007; Cullimore and Johnston 2008; Damour et al. 2016; De Baere et al. 2019; Little et al. 2019; MacLeod et al. 2017;

McNamara et al. 2009; Mugge et al. 2019a; Price et al. 2021; Salazar and Little 2017; Van Landuyt et al. 2022). The same cannot be said about aluminum aircraft wreck sites, which constitute a globally-abundant form of UCH. Considerations of MIC have yet to be applied to submerged aircraft wreck sites (SAWSs), leaving a void pertaining to both the understanding of the microbiomes associated with this site type and the necessary methodological approaches. Thus, this article confronts the latter deficiency by addressing the fundamental issue of microbial sampling. Specifically, a collection study is described, with sampling efforts targeting microbial biofilms, the primary form of SAWS biofouling. Four World War II (WWII)-era SAWSs off the coast of Hawaiʻi were chosen as study sites. The methodological focus of this paper will key in on the use of various sampling implements, step-by-step collection protocols, and downstream considerations related to sample preparation for DNA sequencing. This is prefaced by a brief explanation of SAWSs as heritage resources, and later, an outline of MIC, the expected impacts of climate change, and examples of MIC research in UCH contexts. Specific attention is paid to a lack of non-destructive in situ sampling methods, highlighting the utility of the current study. The article concludes with a discussion regarding the efficacy of the proposed collection method and, ultimately, how microbial data gathered over time is intended to support the management of historic SAWSs. The concept of 'heritage at risk' implies that site managers need not only be concerned with current degradation, but also remain cognizant of the potential ways in which heritage preservation may be comprised moving forward (Hafner et al. 2020). Monitoring changes in site microbiomes, which depend on adequate data acquisition methods, is essential to this effort. It is in this spirit that the article seeks to contribute to archaeological management practices.

The Heritage

The need to develop collection methods pertaining to the investigation of potential MIC impacts on SAWSs was borne out of a desire to protect this heritage resource for future generations. Yet, it is the role aircraft played in the past that justifies the investment in both the efforts described here and studies that build upon this research. During WWII, advancements in aviation technology forever changed the nature of combat and encouraged an emphasis on airpower supremacy (Crane 1993; Deptula 2001; Quester 1978). Today, SAWSs across the globe serve as tangible reminders of this assault in the skies, constituting a considerable portion of UCH inventories. From the United States' (US) perspective, the Navy History and Heritage Command (NHHC) estimates that over 15,000 naval plane wrecks are distributed throughout the world's waters. Aircraft of WWII possess considerable cultural value as, "air power has been memorialized almost exclusively by means of the machines themselves" (Kohn 1995:1052). Submerged aircraft wreck sites act as "touchstones", connecting modern stakeholders with the traumatic events of the past (Gusick et al. 2019:150), as the public is drawn by national pride, historical interests, and an enthusiasm for military remains (Dechow and Leahy 2010; Fix 2011; Wayland 2006).

The historical significance of WWII SAWSs has also imbued these sites with a socio-economic importance. As authentic representations of the war's "chaotic material reality" (González-Ruibal 2008:260), SAWSs often factor into local heritage tourism and wreck-diving industries (Dimmock and Musa 2013; Edney and Boyd 2021; Jeffery 2007; Jeffery et al. 2021; McKinnon 2015). Both enterprises have been promoted as sustainable options for incorporating UCH into commercial agendas, especially in the island states involved in the WWII Pacific Theatre (Collison and Spears 2010; Henderson 2019; Lukman 2020; Scott-Ireton and McKinnon 2015). The SAWSs are framed as part of a "themed diving experience" through their associations with a significant past event (Kirkbride et al. 2013:9). Historical authenticity is often a strong motivation for site visitation (Edney 2012), as Şensurat-Genç et al. (2022:4) reported that over 80% of divers surveyed expressed their preference for vessels that "sank in wars or accidents" over those "intentionally sunk as attractions." This puts a premium on the protection of 'authentic' wrecks, including SAWSs (Edney and Spennemann 2015). For aircraft specifically, site users are also drawn to the novelty of seeing a machine designed for flight, submerged on the seafloor (Edney and Boyd 2021). The wrecks' innate memorialization of airpower is presented in a drastically different environmental context than originally intended. The continued ability for SAWSs to operate as culturally and economically important resources is dependent on appropriate site management strategies that support *in situ* preservation, both now and in the future.

Microbiologically-Influenced Corrosion

Before discussing why MIC was identified as a potential threat to SAWSs, it is important to note that MIC refers to the ability of microbes to alter electrochemical conditions and facilitate increased corrosion through their presence and metabolic activities (Little and Lee 2007:1). For aluminum alloys, such as duralumin (Al2024), the primary construction material of WWII aircraft, previous investigations have suggested that MIC is likely triggered by one of two mechanisms (Ghali 2010:215-262; Little and Lee 2007:139-140; Nelson et al. 2017; Salvarezza et al. 1983). The first is the disrupting effect microbial colonization and activity can have on the protective aluminum oxide film that forms on submerged surfaces. Left alone, this passivating layer is largely responsible for the anti-corrosive properties that make aluminum frequently used in marine engineering (Kaufman 2000:96-117). Specific groups of biofilm microbes, namely sulfate-reducing bacteria (SRB) and marine fungi, have been linked to the MIC of aluminum through the production of metabolites that affect the oxide layer and the underlying aluminum substrate (Dai et al. 2016; de Andrade et al. 2020; Guan et al. 2017, 2020; He et al. 2022; Jaume et al. 2022; Javed et al. 2017; Wang et al. 2019). The second MIC pathway involves the formation of an oxygen concentration cell, where the deoxygenated aluminum under a respiring biofilm colony becomes anodic, releasing metal ions as electrons move to more oxygenated surfaces (Van Loosdrecht et al. 2002).

Though these mechanisms offer insights into how MIC could theoretically impact SAWSs, straightforward interpretations and predictions are complicated by factors that affect both the MIC process and the microbes responsible. The use of alloying constituents, namely copper for WWII aircraft (Ouissi et al. 2019), in differing percentages can impact how an aluminum alloy corrodes (Berzins et al. 1977; MacLeod 1983), while also influencing microbial colonization (Zhai et al. 2022; Zhang et al. 2019a, 2019b). Additionally, biofilms on submerged aluminum surfaces, including those containing SRB, are not always linked to increased degradation. In some cases, experiments revealed that biofilms can inhibit aluminum corrosion (Gao et al. 2021; Guan et al. 2020; Mansfeld et al. 2002; Örnek et al. 2002; Shen et al. 2020). Thus, the overall corrosive effect that marine biofilms may have on SAWSs, as inferred through observations of microbial impacts on modern aluminum alloys, is difficult to discern. While these nuances are undoubtedly important for understanding both MIC and its relevancy to UCH management, the methodological focus taken here is mainly concerned with formulating monitoring strategies designed to broach questions of MIC and other biofilm related interests. For those seeking to draw their own conclusion regarding the likelihood of MIC impacting SAWSs, interested readers are redirected to one of the treatises on the molecular and biological principles of MIC cited above.

The complexity of MIC makes predictions of how this preservation threat affects SAWSs in a future defined by climate change even more difficult. Dobretsov et al. (2019) provided a thorough synopsis of the ways in which biofouling organisms, including microbial biofilms, are expected to respond to increases in the ocean's temperature, acidification, turbulence, and pollution. The impact that any one of these changes has on biofilms can include shifts in the taxonomic makeup, metabolic activity, and bioactive molecules (Baragi and Anil 2016; Ng and Chiu 2020; Somma et al. 2023; Toyofuko et al. 2016; Witt et al. 2012a). Though studies explicitly examining the connection between MIC and climate change are limited (Puentes-Cala et al. 2022; Tuck et al. 2022a), research on changing environmental conditions has yielded credible evidence as to how the prevalence of MIC may be impacted in the future. For example, increased temperatures and nutrient levels that are expected with anthropogenically-induced climate change are believed to stimulate heightened activity of mesophilic microbes within biofilms, including some linked to MIC (Khosravi et al. 2019; Lawes et al. 2016; Mensch et al. 2020; Price and Sowers 2004; Russell et al. 2013; Salgar-Chaparro et al. 2020; Stratil et al. 2013; Wahl et al. 2012; Witt et al. 2012b). Research on ocean acidification is less prone to generalizations, suggesting that the impact of elevated carbon dioxide partial pressure (pCO_2) has a more taxa-specific effect on biofilm communities (Allen et al. 2021; Das and Mangwani 2015; Kerfahi et al. 2023; Patil et al. 2011; Webster et al. 2013; Witt et al. 2011). The concurrence of factors only further complicates the situation, leading Dobretsov et al. (2019:588) to succinctly conclude that the combined effect is "rather unpredictable."

Microbiologically-Influenced Corrosion and Underwater Cultural Heritage

While SAWSs have yet to be the subject of research investigating MIC, this topic has been examined in a variety of other UCH contexts. This includes the steel shipwreck sites referenced above, as well as sunken munitions (Cybulska et al. 2020; Silva and Chock 2016:14) and historical marine infrastructure (Melchers and Jeffrey 2012, 2013; Usher et al. 2014). These studies have led to a rethinking of how the natural environment places certain heritage at risk. No longer a niche subcategory, wreck ecology constitutes a *bona fide* research pursuit that has yielded pertinent information on taxonomic composition and functional gene profiles. The intersection of microbial colonization and site corrosion has resulted in a range of interpretations, from fears regarding the "biological extraction" of wreck metals (Church et al. 2007:206; Cullimore et al. 2001:126), to site impacts correlating with contaminant exposure (e.g. oil spill) and the subsequent change in the microbes and genes present (Mugge et al. 2019a, 2019b, 2021; Salerno et al. 2018). In some cases, the occurrence of MIC was empirically refuted (Little et al. 2019; Salazar and Little 2017), while other studies identified taxonomic associations with corrosion products and biocorroders (Price et al. 2021; Sánchez-Porro et al. 2010; Usher et al. 2014). Studies from the Gulf of Mexico have recently expanded this line of research to include the potential effect that wreck biofilm dispersal has on the colonization of new seafloor installations (Mugge et al. 2023a, 2023b). The often overlooked impact that wreck sites have on the 'background microbiome' (Hamdan et al. 2021:2889), including the promotion of microbes that facilitate corrosion, can inform decisions on where to situate pipelines, oil rigs, and other offshore infrastructure susceptible to MIC.

However, the collection methods utilized exhibit a glaring deficiency in terms of non-destructive *in situ* sampling. Most often, corrosion and marine concretion samples, including the famed rusticles of RMS *Titanic* (Cullimore and Johnston 2008; Salazar and Little 2017; Stoffyn-Egli and Buckley 1995), are transported to laboratories. There, microbial genetic material can be isolated for DNA sequencing (McNamara et al. 2009), while visual analyses (e.g. scanning-electron microscopy) are employed to characterize a sample's physiochemical properties (Albahri et al. 2019). Alternatively, test coupons and other biofilm recruitment arrays have been placed on-site, serving as a proxy for the actual wreck substrate (Cullimore and Johnston 2008; Mugge et al. 2019a). In two recent examples, Price et al. (2021) collected loose shipwreck debris and took drilled core samples from a WWII-era landing craft wreck, while Van Lan Landuyt et al. (2022) recovered two wreckage pieces from the V-1302 *John Mahn* (1942). The authors of both studies obtained microbial samples by scraping and swabbing the shipwreck fragments in a laboratory setting. In their study of long-term corrosion rates associated with 20th century shipwrecks, De Baere et al. (2019:11) articulated the point that the *in situ* preservation ethos, combined with legal restrictions and international agreements (e.g. 2001 UNESCO *Convention on the Protection of Underwater Cultural Heritage*), can make it "morally and legally impossible to collect pieces of shipwrecks." The authors, however, noted that "destructive sampling was needed" in order to "obtain a clear view on the possible influence of MIC" (De Baere et al. 2019:11). Thus, they opted to recover an unprovenanced piece of historic anchor chain as a substitute for this analysis. The lack of non-destructive *in situ* sampling methodologies highlights the need for effective microbial collection methods that are both minimally-invasive and capable of yielding relevant genetic information.

Methodology

This study sought to develop a methodology for collecting *in situ* biofilm samples from SAWSs for the purposes of microbial DNA sequencing. Pochon et al. (2015) expressed a similar research objective when comparing four implements (syringe, swab, tape, and sponge) used in the collection of marine biofilms from glass collection plates. DNA concentration and sequence yields helped to infer success or failure (e.g. DNA from tape failed to amplify for sequencing).

Upon consultation with Dr. Xavier Pochon (Cawthron Institute, New Zealand), as well as Dr. Gail Ashton (Smithsonian Environmental Research Center), who performed similar biofouling studies (e.g. Clark et al. 2019), it was decided that this project would assess the feasibility of using syringes to collect SAWS biofilm. Significant consideration was given to the time required, financial costs, and practicalities of working underwater. Syringes seemed preferrable to other collection tools (e.g. sponges, swabs, and tape) given their suction capabilities, which would aid in gathering dislodged biofilm in an aquatic setting. Furthermore, the syringe volume, 50 milliliters (mL), enables increased biofilm collection, as opposed to being limited by surface area (e.g. sponge or swab). Four sites off the coasts of Maui (Curtiss SB2C-1C Helldiver and Grumman F6F-3 Hellcat) and Oʻahu (Republic P-47 Thunderbolt and Vought F4U Corsair) were chosen (Figure 3.1). Each has been described in previous reports (Bush 2023; Bush et al. 2023; National Oceanic Atmospheric Administration [NOAA] 2011, Petrey et al. 2008). The sampling method's efficacy was assessed using DNA concentrations and sequencing results. Fieldwork in Māʻalaea Bay, Maui was carried out by a team of archaeologists and biologists from East Carolina University, while a local non-profit organization, Naval Exploration and Research Divers, assisted collections in Waimānalo Bay, Oʻahu. Financial support was provided by a National Center for Preservation Technology and Training Grant from the National Park Service (NPS) (P19AP00137).

Sample Collection

Prior to sample collection, each site, besides the Corsair, was photogrammetrically surveyed using underwater cameras. The resulting imagery was used to make digital models (Agisoft Metashape v1.8), which served as 3D sampling maps (Figure 3.2). Biofilm sample collection was done by a team of three SCUBA divers, which began by placing a 10 × 10 centimeter (cm) grid-square at the desired location.

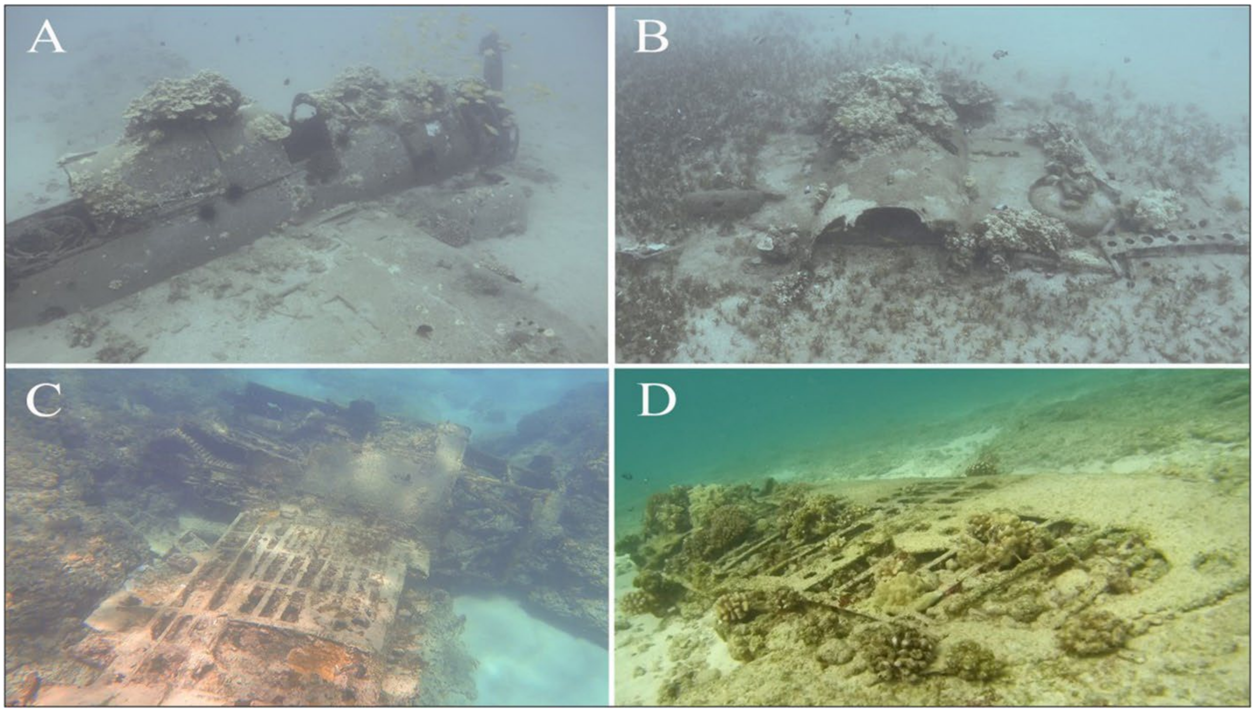

Figure 3.1. The four study sites: (a) Curtiss SB2C-1C Helldiver (Maui); (b) Grumman F6F-3 Hellcat (Maui); (c) Republic P47 Thunderbolt (Oʻahu); (d) Vought F4U Corsair wing (Oʻahu). (Photos courtesy of East Carolina University/Naval Exploration Research Divers, 2021)

Sampling locations concentrated on exposed (i.e. lacking macrofouling) aluminum that provided sufficient surface area (>100cm^2). For this initial collection, sampling locations (10) were divided evenly amongst visibly-corroded and non-corroded surfaces (Figure 3.3). Following pre-disturbance photographs, one diver dislodged the biofilm with a polypropylene spatula, while avoiding damage to the aluminum surface. Simultaneously, another diver extracted a 50 mL syringe fitted with a 1 cm tubing attachment. Capturing as much biofilm material as possible, divers used three syringes per sampling square (Figure 3.4). Though aluminum is the focus of this study, time permitted for additional biofilm collection at the Hellcat site from two non-aluminum surfaces, a rubber tire and a stainless-steel fitting. Additionally, researchers experimented with collection tools at this site, using WhirlPack Sponge Probes to gather three biofilm samples from aluminum surfaces. This collection method used the same 100 cm^2 sampling grid. On average, 5-6 biofilm samples were taken on a single tank dive, which lasted between 45-60 minutes.

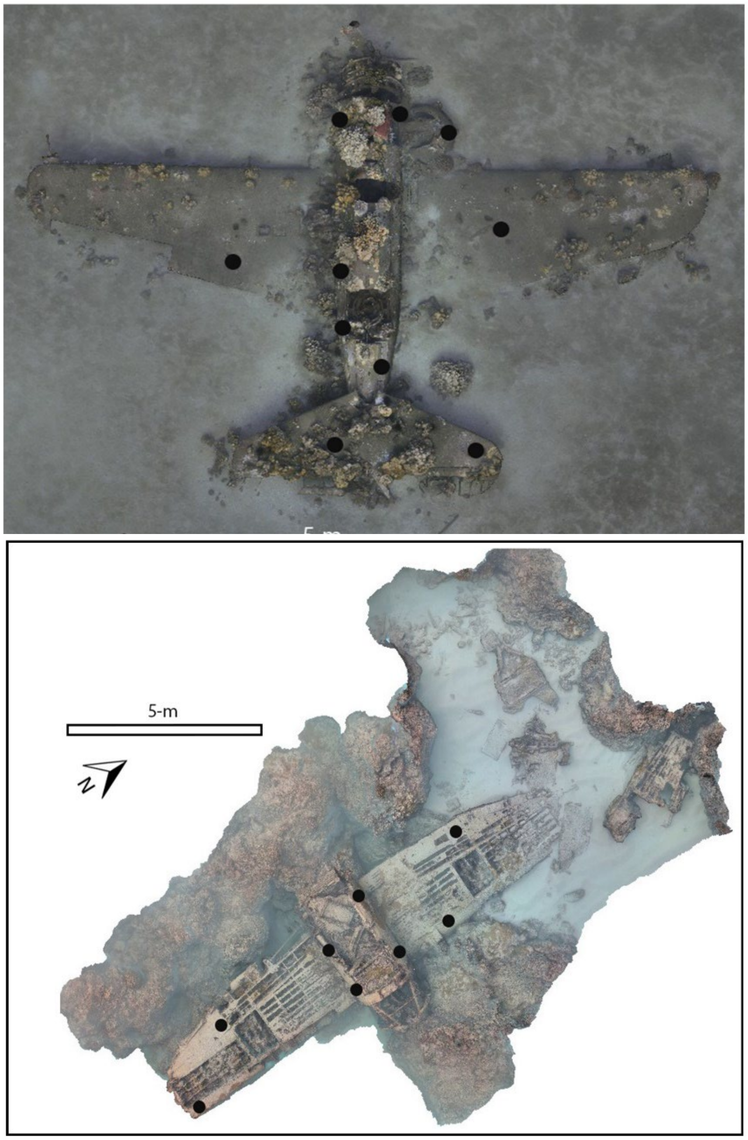

Figure 3.2. 3D models of Helldiver site (top) and Thunderbolt site (bottom) with sampling locations indicated by black dots. (Models by the author, 2022)

The project team also took sediment and seawater samples from each site. While the sequencing data can eventually be used to understand the effects that wrecks and the surrounding environment have on each other's microbiome, for this study, these samples served as a control. Unlike the uncertainty regarding whether syringes would obtain adequate genetic material, sediment and seawater samples were collected using well-established methods. Thus, the resulting data (i.e. DNA concentrations, sequencing success, and bacterial sequence counts) can help infer the validity of the biofilm dataset. Statistically similar results across sample types would indicate a successful biofilm collection.

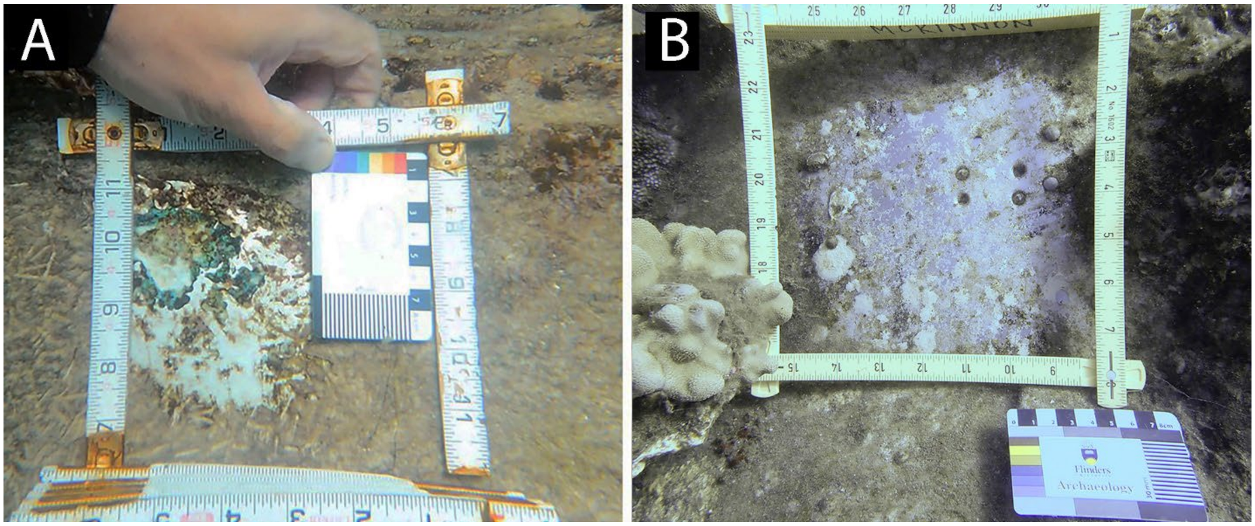

Figure 3.3. Examples of wreck surfaces samples: (a) blue/green copper corrosion (Thunderbolt site, O‘ahu); (b) non-corroded (Helldiver site, Maui). (Photos by the author, 2021)

For sediment, divers collected samples in 50 mL falcon tubes from four areas at each site: near a visibly corroded aluminum surface, near a non-corroded aluminum surface, 5 meters (m) from the wreck, and 30 m from the wreck. An additional sediment sample was taken from underneath the Helldiver's fuselage and an algae-covered sand patch near the Hellcat. Three 1 liter water samples were collected into sterilized plastic containers from above each site. Water samples were then filtered using a 0.2 micrometer Polyethersulfone filter placed into a plastic holder. The holder was attached to a syringe, so that the water samples could be filtered through in 50 mL intervals. Each filter was then aseptically transferred to a falcon tube. Samples were kept frozen and shipped on ice to East Carolina University's Howell Science Complex, where they were placed in a -20°C freezer until DNA extractions.

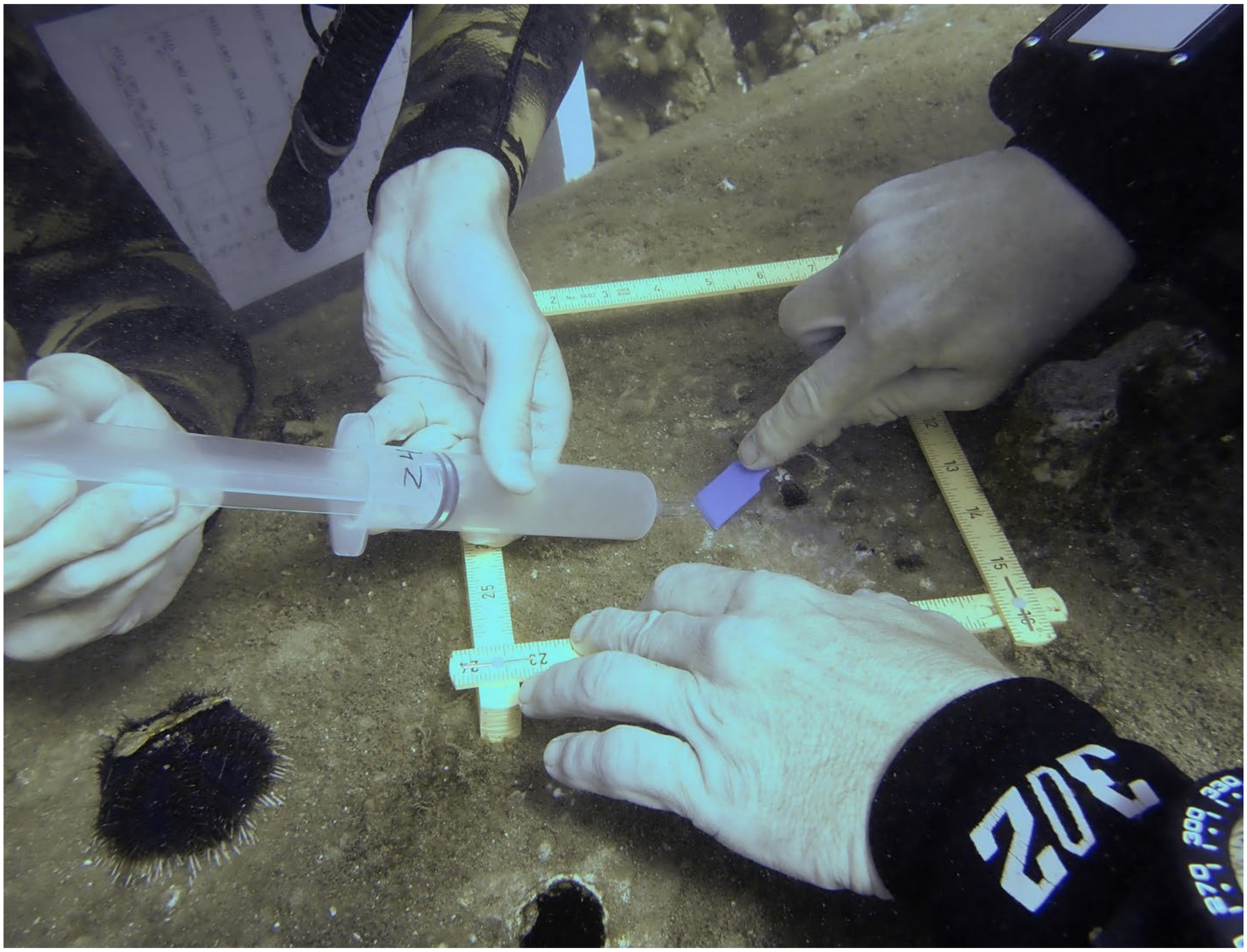

Figure 3.4. Photo of biofilm sampling method developed during this study. Hellcat site (Maui). (Photo courtesy of East Carolina University, 2021)

DNA Extractions

All sediment and biofilm samples were processed using the DNeasy PowerSoil Pro kit, due to its availability and proven track record. For biofilm samples, a 100 microliter pipette was inserted into the settled biofilm material at the bottom of the falcon tube, minimizing the amount of seawater placed into the extraction kit's lysis tube. For sediment samples, excess seawater was poured off and subsamples were loaded into lysis tubes using metal spatulas. Six biofilm samples were reprocessed using the DNeasy PowerBiofilm kit, as a way of testing whether one kit was more effective in isolating microbial genetic material from biofilm (e.g. Dauphin et al. 2010). The DNeasy PowerWater Kit was used for all water samples, as it is designed specifically to isolate genetic material from water filters. To ensure each extracted sample met the minimal yield threshold for sequencing (1 nanogram/microliter (ng/μL)), DNA concentrations were assessed using a Qubit Fluorometer. Ten microliter subsamples were shipped to Integrated Microbiome Resource (IMR), where they were sequenced using an Illumina MiSeq. This method produces millions of reads per run on a specified region of DNA, which provides greater coverage from the perspective of community-level statistics (Quail et al. 2012). Sequencing targeted the V4-V5 region of the 16S rRNA gene due to its ubiquity in bacteria and diagnostic nature (Schmalenberger et al. 2001), which make it the most widely studied 16s rRNA region.

Results

DNA Concentration Yields

A total of 75 samples were collected: 45 biofilm (three by the sponge method), 18 sediment, and 12 water filters. For biofilm and sediment samples, a minimum of 0.25 grams (0.4-0.5 preferrable) was needed for the two DNA extraction kits. Biofilm weights were of particular interest, as obtaining an adequate amount of material was a concern prior to fieldwork. Each syringe-collected sample, however, produced more than the material threshold. The surplus biofilm was needed, as eight extractions originally failed to yield sufficient DNA. Several sediment samples were also unsuccessful at first, and the extraction process had to be repeated.

All water samples passed the concentration check initially. Besides the third sample obtained with the WhirlPack Sponge, at least 1 ng/µL of DNA was successfully obtained from each sample, including those from the stainless-steel fitting and rubber tire (Table 3.1). In general, the sponges collected little biofilm material, which precluded repeated extractions. Similarly, DNA concentrations from the other two sponge samples were relatively low. Biofilm samples collected using the syringe method produced an overall mean DNA concentration of 8.25 ng/µL, which was significantly higher (t=3.63; p=.001) than the mean produced by sediment samples (n=18; mean=3.03), while being nearly equal with that of seawater samples (n=12; mean=8.33). The minimum and maximum values of all three sample types compared favorably. DNA yields were not improved by using the PowerBiofilm kit for biofilm samples (n=6; mean=2.86), thus, to eliminate any potential biases that could arise from using different kits, the PowerSoil Pro kit was used for final extractions.

DNA Sequencing

Of the samples submitted to IMR, 90.1% (73 of 81) were successfully sequenced, including six that were resubmitted after the first sequencing attempt failed (Table 3.1). The lone sample that could not be sequenced was a biofilm sample from the Thunderbolt site. Sequencing reads were returned as fastq files, which were then imported into mothur v1.41.3 [https://mothur.org/], an open-source, bioinformatics data processing software. Following an updated version of protocols by Schloss et al. (2013), nucleotide sequences were translated into operational taxonomic units (OTUs), which are used as proxies for traditional taxonomic ranks. Sequences that read at a similarity threshold (97% in this study) for the designated marker gene (16S rRNA) were clustered into a single OTU. The sample OTUs were then identified taxonomically by comparing sample sequences with reference examples (silva v.132 database), which will enable future assessments of community composition.

Table 3.1. Sample List

Sample ID	Location	Type	Material	DNA Yield Range	Average Sequencing Counts
DNeasy PowerSoil Pro Kit					
1-5	Maui: Hellcat	Biofilm	Aluminum, Corroded	3.19 – 19.8	95,986
6-10	Maui: Hellcat	Biofilm	Aluminum, Non-Corroded	4.2 – 9.06	50,978
11	Maui: Hellcat	Biofilm	Rubber, Tire	2.01	4,358
12	Maui: Hellcat	Biofilm	Stainless Steel, Fitting	1.38	4,297
13-15[a]	Maui: Hellcat	Biofilm (Sponge)	Aluminum, Non-Corroded	.07 – 3.83	6,737
16-20	Maui: Helldiver	Biofilm	Aluminum, Corroded	2.45 – 9.38	15,005
21-25	Maui: Helldiver	Biofilm	Aluminum, Non-Corroded	2.67 – 12.5	24,266
26-30	O‘ahu: Corsair	Biofilm	Aluminum, Corroded	6.79 – 27.0	69,190
31-35[b]	O‘ahu: Corsair	Biofilm	Aluminum, Non-Corroded	1.04 – 25.8	68,664
36-40	O‘ahu: Thunderbolt	Biofilm	Aluminum, Non-Corroded	5.9 – 11.9	89,693
41-45	O‘ahu: Thunderbolt	Biofilm	Aluminum, Non-Corroded	5.63 – 10.9	95,611
46-50	Maui: Hellcat	Sediment	Sediment	1.44 – 12.7	43,083
51-55	Maui: Helldiver	Sediment	Sediment	1.06 – 5.08	8,766
56-59	O‘ahu: Corsair	Sediment	Sediment	1.38 – 2.63	33,494
60-63	O‘ahu: Thunderbolt	Sediment	Sediment	1.35 – 2.3	51,978
Dneasy PowerBiofilm Kit					
1	Maui: Hellcat	Biofilm	Aluminum, Corroded	1.3	N/A
7, 9, 10	Maui: Hellcat	Biofilm	Aluminum, Non-Corroded	2.37 – 5.01	N/A
11	Maui: Hellcat	Biofilm	Rubber, Tire	1.84	N/A
12	Maui: Hellcat	Biofilm	Stainless Steel, Fitting	2.32	N/A
Dneasy PowerWater Kit					
64-66	Maui: Hellcat	Seawater	Seawater	8.11 – 15.2	11,271
67-69	Maui: Helldiver	Seawater	Seawater	14.2 – 18.8	11,598
70-72	O‘ahu: Corsair	Seawater	Seawater	2.49 – 3.47	116,348
73-75	O‘ahu: Thunderbolt	Seawater	Seawater	2.19 – 4.02	116,313

a: DNA concentration of Sample 15 below sequencing threshold and could not be reextracted
b: Sample 31 failed to sequence

Across the 73 total samples, 3,306,515 bacterial sequences were identified after quality filtering. For each sample type, sequences counts were higher for the Oʻahu samples than the Maui samples. Sequence counts from the Maui biofilm samples were not significantly different than either sediment (t= -1.11, p=0.277) or seawater (t=1.01, p=0.324). Conversely, Oʻahu biofilms yielded significantly higher sequence counts when compared to sediment samples (t=2.54, p=0.018), while the opposite was observed as it pertains to comparisons with seawater samples (t= -1.89, p=0.072). Despite these interisland differences, it appears that biofilm collection was successful.

Discussion

Before the relevancy of MIC to SAWSs can be analytically assessed, effective collection methods are needed, specifically, for obtaining *in situ* biofilm samples. As discussed, proxies for wreck microbiomes, including test coupons, have yielded valuable insights into the effect MIC has on UCH sites. However, the intricacies of microbial colonization and the microscopic scale in which differences can manifest warrants consideration. Though duralumin was the principal alloy, the metallurgic composition of WWII aircraft is far from homogenous. This not only varied by country and plane type, but also by component (e.g. frames and skins), which required separate manufacturing techniques (e.g. extrusion, rolling, and casting) and stress resistances (Ouissi et al. 2019). Thus, different variations of aluminum alloys were used, which are likely to yield microbial biofilms with differing constituents and functional genes. This should encourage site managers to acquire as authentic an interpretation of a site's microbiome as possible. Yet, the removal of wreck components is imbued with ethical and legal complications, which may negate this form of sampling. Even if it is justified as a way of establishing a foundational understanding of MIC mechanisms, routine monitoring efforts require less destructive means of sample collection.

To that end, this study succeeded in creating a sampling method that produced sufficient microbial genetic material from biofilm, as inferred by comparisons with sediment and seawater samples. Biofilm sampling was uncertain, given its limited concentration (1 millimeter thick layer) on wreck surfaces. Yet, sample weights, DNA yields, and sequencing success indicate that the syringe method of collection can be used for future SAWS biofilm studies. Beyond the primary collection method, two additional aspects of the current study warrant further discussion. The first is the attempt to use a different collection device, a WhirlPack sponge. In this study, sponge collection resulted in noticeably less biofilm material and is not recommended for future use. The second methodological insight pertains to DNA extraction kits. For the current study, there were concerns about the ability of the PowerSoil Pro kit to extract sufficient genetic material from biofilm, when compared to the PowerBiofilm kit. No appreciable differences in DNA quantity were observed; as such the PowerSoil Pro kit was ultimately chosen, as it will allow for the most appropriate taxonomic comparison between sediment and biofilm samples.

The biofilm collection procedures had to account for the practicalities of working underwater and be amenable to use by SCUBA divers. Biofilm samples were not only obtained in a relatively straightforward process, but also done so economically in terms of time. The project team spent a maximum of two one-hour dives at each site, resulting in the collection of 10-12 biofilm samples per site. The current study strove to be efficient, minimally invasive, and affordable, while still capable of yielding relevant information. This intention was not only done out of concern for the Hawaiian SAWSs chosen as sampling sites, but originated from the hope of making *in situ* biofilm sampling a viable option for site management agencies. By doing so, baseline collection efforts, such as the one presented here, as well as subsequent monitoring projects become feasible.

Ultimately, this collection method is meant to support research related to both the current understanding of SAWS microbiomes and how these may shift in response to climate change, without compromising the heritage resources. An inspection of the Thunderbolt site 14 months after fieldwork indicated that there were no obvious adverse effects from the initial sampling effort. The lack of specialized equipment for *in situ* sampling makes biofilm collection more practical. The plastic syringes and falcon tubes used can be purchased in packs of 40-50 for less than $100 USD. Other supplies, including the polypropylene spatulas, serological pipettes, and syringe filter (for water sampling), can also be purchased for reasonable amounts. This methodology has been shared with the NOAA, NPS, Hawai‘i State Historic Preservation Division, and NHHC. The last of these agencies has already expressed explicit interest in follow up biofilm collections, in hopes of better understanding the microbial communities associated with the UCH resources they manage.

The use of inexpensive collection materials and a reproducible order of operations may also facilitate collaborations with ‘citizen scientists’, which are defined as “a volunteer who collects and/or processes data as part of a scientific enquiry” (Silvertown 2009:467). For SAWSs, the recreational diving community stands out as a capable and motivated group, given their vested interest in the continued survival of the UCH sites they frequent (Viduka and Edney 2022). Furthermore, recreational divers are often keen observers of site transformations, with insights that can inform scientific interpretations (Viduka 2022). Communication with these divers and other stakeholders can be used to articulate not only how to collect biofilm, but also why these samples aid site management. This transparency should prevent temporary evidence of past collections serving as an invitation for unwanted contact with SAWSs. In the current study, Naval Exploration Research Divers (NERD), a collaborative non-profit made up of local archaeologists and recreational divers, proved to be an invaluable research ally. With access to their own watercraft and SCUBA equipment, NERD volunteers are fully capable of repeating the microbiological surveys, if given the requisite collection materials. The possibility of follow-up studies aimed at additional wreck sites and seasonal influences has been discussed with NERD. This kind of knowledge transfer may help local communities develop a stronger sense of stewardship towards UCH resources (Viduka 2020). For non-local researchers, project costs are greatly reduced by not needing to return for sample collection. Admittedly, the expenses associated with the laboratory analysis, both in terms of consumables (e.g. DNA extraction kits) and equipment, likely negates the ability of management agencies and citizen scientists to perform this portion of the project. In such cases, partnerships with academic institutions who have access to the requisite facilities offer a way forward.

While the current study has documented an effective means of sampling biofilm from SAWSs, it is the potential of the taxonomic data that is perhaps most consequential. Sample areas were chosen on the basis of observed corrosion, which is intended to eventually elucidate differences between the bacterial communities associated with corroded and non-corroded aluminum surfaces. Given the metallurgically-complex makeup of aircraft, subsequent sampling efforts can target other areas to discern how additional factors, such as aluminum alloy type, surface treatments, and chemical residues, affect microbial colonization. The interpretation of these results should allow for a more informed assessment of both the microbes currently colonizing the SAWSs and which additional lines of microbiological evidence (e.g. metagenomic studies of gene profiles) are needed for determining the potential of MIC. Yet, this initial sampling effort is likely to only offer a snapshot. The taxonomic data, when available, should not be viewed as a definitive characterization, nor evidence of any conclusive links between the marine microbiota and heightened corrosion. Instead, site managers armed with a baseline understanding of each wreck's microbiome, should perform repeated follow-up biofilm collections that are paired with photogrammetric surveys and electrochemical corrosion assessments to track potential correlations between increased site degradation and microbial communities.

Such an approach was utilized in the documentation of *U-166*'s corrosion following the *Deepwater Horizon* oil spill in 2010, where time series images indicated significant metal loss (Damour et al. 2019). The visual evidence of deterioration was coupled with assessments of the microbes and genes present within biofilms formed on nearby steel recruitment arrays, which exhibited similar metal loss. This suggested a link between the sunken submarine's increased corrosion and microbes likely colonizing its surface in the wake of the oil spill (Mugge et al. 2019a). For SAWSs, the development of a practical and efficient method of collecting *in situ* biofilm samples without significantly impacting the heritage resources makes this a more realistic possibility. From there, site managers can begin to proactively consider mitigation responses. Yet, the *U-166* example demonstrates that before the questions of 'how' to inhibit MIC can be considered and the degree to which management agencies should invest in mitigation measures, the questions of 'who' may be contributing to MIC and to what extent is this phenomenon actually manifested must be broached.

There are those who may remain wary of the importance of assessing the potential for MIC and the need for mitigation, especially when a scarcity of time, funding, and personnel is combined with a multitude of site management priorities. For SAWSs, the questioned significance is made even more suspect by the lack of data regarding the relevance of MIC to this site type. Given this uncertainty, it would be misleading to imply that MIC is the most pressing threat to SAWS preservation. Evidence from corrosion surveys of WWII SAWSs off the island of Saipan suggests that galvanic corrosion, resulting from aircraft components with differing metallurgic properties being in electrical contact with one another, is a more immediate concern (Richards and Carpenter 2018). Other monitoring efforts associated with these SAWSs indicated that extreme weather events, which are likely to increase in frequency due to the on-going climate crisis, are also currently affecting sites (McKinnon et al. 2018). Additionally, anthropogenic impacts, including recreational diving and anchoring, were noted as detrimental to SAWS preservation in Saipan (McKinnon 2015; McKinnon and Carrell 2014; McKinnon et al. 2018). Therefore, it should be emphasized that MIC research is not the only utility for *in situ* biofilm collections. Success in isolating environmental or extracellular DNA (eDNA) from biofilms has enabled several environmental monitoring studies focused on key aquatic species (Rivera et al. 2022, 2023; Tuck et al. 2022b; Wood et al. 2020). Recently, the sampling methodology presented here was incorporated into a multi-disciplinary assessment of the aforementioned Saipan SAWSs (NOAA 2023). While the microbial data ascertained may be used to further an understanding of the potential of MIC, the primary purpose was gathering information on biodiversity and discerning the artificial reef role of SAWSs.

Finally, climate change necessitates the pursuit of baseline knowledge regarding wreck microbiomes. Such information can aid in understanding ecological impacts and how microbial changes affect the corrosion process. In researching the effect rising temperatures have on UCH corrosion, North and MacLeod (1987:74) conceded that the exact relationship is “complicated by [temperature’s] effect on biological growth.” Melchers (2014) illustrated this via a multi-phase corrosion model, contrasting linear corrosion rates with MIC prevalence, a nonlinear variable dependent on temperature, pH, and nutrient concentration. As discussed above, the forecasted shifts in ocean conditions associated with global climate change, namely rising sea surface temperatures, acidification, and eutrophication, are likely to correlate with changes to microbial communities, both taxonomically and functionally. Climate-induced ecological shifts that affect historic preservation have already been observed at the macroorganism level, including zebra mussels in the Great Lakes (US and Canada) and shipworms in British waters (Dunkley 2015; Watzin et al. 2001; Wright 2016). Just as site managers have tracked modifications to these species' ranges and the corresponding impact on UCH, changes to site microbiomes must also be considered. Microorganisms, previously less equipped for certain temperatures and pH levels, may be able to take advantage of increased temperature and acidification through competition and successful metabolic adaptations. Monitoring these changes and their causes through baseline studies that use collection methodologies such as the one presented here is vital to eventually determining if shifting wreck microbiomes affect SAWS preservation.

Conclusion

Aircraft of WWII possess an inherent significance due to a range of factors, including feelings of nostalgia and reverence, regulatory mandates, and correlations with deceased servicemembers. Additionally, SAWSs can support heritage tourism and diving industries. Yet, there remains a significant research void concerning how microorganisms affect SAWS corrosion, though MIC has been studied in other UCH contexts. While data from these studies have been informative, the methodologies often rely on destructive sampling techniques and proxies for wreck microbiomes. To rectify this situation, this paper presented the first attempt to collect microbial DNA from four SAWSs off the coast of Hawaiʻi. The sampling methodology was designed specifically for use by SCUBA divers and was proven to be both cost and time-efficient. The initial results, including sample weights, DNA yields, and sequencing success highlight the feasibility of the collection and DNA extraction processes. Establishing practical survey protocols is a necessary first step in monitoring how MIC may be impacting SAWSs. From there, citizen science collaborations and the incorporation of MIC surveys into site management best practices are made possible. Additionally, *in situ* biofilm collection is not exclusive to MIC research. Those interested in wreck biofilm communities for reasons pertaining to marine biodiversity and the artificial reef role of UCH sites may also find the collection methodology put forth useful. A foundational understanding of which microbes are present on SAWSs, and the environmental factors influencing these communities, is now especially warranted. As changing ocean conditions will undoubtedly alter microbial distribution, it is imperative that archaeologists consider the totality of forces, including those at the microscopic level, that place heritage at risk.

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Chapter 4: The Microbiomes of World War II Submerged Aircraft Wreck Sites Off Maui and Oʻahu

ABSTRACT

The impact that microorganisms have on underwater archaeological sites has recently drawn significant interest, prompting numerous research efforts. These investigations, however, have yet to consider the potential effect microbiologically-influenced corrosion has on historic submerged aircraft wreck sites made of aluminum. Past studies of microbial biofilms, the primary form of biofouling associated with these sites, suggests that taxonomic composition may exhibit substrate-specific tendencies, though a larger effect has been attributed to environmental factors that dictate species sorting processes. In order to assess the extent to which substrate and environment influence biofilm composition, and how this may facilitate microbiologically-influenced corrosion, four World War II-era aircraft wrecks off the coast of Hawaiʻi were chosen for biofilm sampling and DNA sequencing. The results demonstrated that the bacterial communities found on the wreck surfaces were taxonomically distinct from those of the surrounding seawater and sediment. Comparisons amongst the four sites helped to elucidate information on the dominant and unique taxa affiliated with submerged aircraft wreck sites biofilms, while highlighting the ways, both expectedly and unexpectedly, that the environment shaped the microbial communities. Though no concrete evidence of microbiologically-influenced corrosion could be discerned from these results, there are several taxonomic patterns that warrant further investigation.

Key Words: Microbiologically-Influenced Corrosion, Aluminum, Biofilm, Historic Aircraft

Introduction

During World War II (WWII), the strategic emphasis on airpower supremacy (Hansell 1986) spurred unparalleled levels of aircraft production (Morgan 1994; Office of Statistical Control 1945). Today, tangible evidence of this assault on the skies can be seen in the many submerged aircraft wreck sites (SAWSs) that populate the world's seafloors. As symbols of aviation history and military sacrifice, SAWSs factor prominently into the diving tourism industry and represent a finite resource whose continued preservation warrants careful consideration (Bush 2021; Edney and Boyd 2021; Makmur et al. 2020; McKinnon 2015). The latter is aided by an understanding of the natural threats these wrecks face, which requires an evaluation of how the physical materials that make up an aircraft interact with the surrounding environment. Recently, there has been an increased recognition of the role microbiologically-influenced corrosion (MIC) plays in the preservation of submerged historic resources (Melchers 2021; Moore 2015; Paxton et al. 2024). Here, MIC refers to the ability of microorganisms to increase corrosion rates by altering a substrate's microenvironmental conditions (Little and Lee 2007). This line of research, however, has yet to be extended to SAWSs, which are primarily made of aluminum. Though understanding the chemical processes of submerged aluminum corrosion is important, the focus henceforth will be on the microbiological aspect. Interested readers are redirected to one of the many in-depth discussions of aluminum corrosion theory (Berzins et al. 1977; Davis 1999; Dix et al. 1975; Goodard et al. 1967; MacLeod 1983) and the molecular principles of related MIC (de Andrade et al. 2019; Dexter 1987; Ghali 2010; Guan et al. 2017; Jaume et al. 2022; Nelson et al. 2017).

The MIC of submerged archaeological sites has been studied in various forms of attached communities, including rusticles, microbial concretions, biofilm, and sea snow (Albahri et al.

2019; Church et al. 2007; Damour et al. 2016; De Baere et al. 2021; Little et al. 2019; McNamara et al. 2009; Mugge et al. 2019a; Overfield 2005; Price et al. 2021a; Salazar and Little 2017; Stoffyn-Egli and Buckley 1995; Van Landuyt et al. 2022). Biofilms, however, are the most germane to submerged aluminum, as evidenced by the presence of a "mucilaginous layer" (biofilm) noted during generalized corrosion surveys of SAWSs (MacLeod 2006:128; Richards and Carpenter 2015). Biofilms are composed of microbial communities, naturally-produced adhesives (e.g. extracellular polymeric substances), and corrosion products (e.g. metal ions, oxidized metal) (Beech 2004; Costerton et al. 1995; Dobretsov 2010; Fang et al. 2002). Oxygen gradients form as the microbes in the outer sections metabolize dissolved oxygen from the surrounding seawater (Flemming et al. 2001; Smart et al. 2008). This can result in complimentary niches that facilitate metabolism through the creation of microenvironmental conditions and molecular exchanges that support metabolism (Dang and Lovell 2016; De Carvalho 2018; Dussud et al. 2018; Salta et al. 2013; Tuck et al. 2022; Wuertz et al. 2004). Microbial activity associated with marine biofilms, primarily the production of corrosive metabolites (e.g. sulfides) and the formation of oxygen concentration cells, have been linked to MIC (Little and Lee 2007, 2014, 2022; Little et al. 2008).

Biofilm microbiomes associated with submerged historic resources, specifically steel shipwrecks, have been investigated in terms of the potential for increased corrosion (Damour et al. 2016; De Baere et al. 2021; Hamdan et al. 2018; Mugge et al. 2019a; Overfield 2005; Price et al. 2021a; Van Landuyt et al. 2022). However, using these studies as analogs for understanding potential MIC pathways for aluminum-based aircraft ignores the observed role that substrate material plays in shaping attached microbial communities (Kim et al. 2021; Li et al. 2014a; Mohamed et al. 2023; Oberbeckmann et al. 2016; Witt et al. 2011). Research from within the field of heritage preservation found significant differences in the taxonomic composition of biofilm communities colonizing different substrates (steel and wooden) placed near historic shipwrecks in the Gulf of Mexico (GOM) (Hampel et al. 2022; Moseley et al. 2022; Mugge et al. 2019a, 2023a, 2023b). Similarly, Price et al. (2021a), analyzed the bacterial communities from differing surfaces on a single steel shipwreck, noting contrasts between shipwreck debris with and without corrosion. This included higher relative abundances of iron-oxidizing Zetaproteobacteria from corroded contexts, which provided further evidence of taxa-specific associations between marine microbes and iron corrosion products (Garrison et al. 2019; Li et al. 2014b; McBeth and Emerson 2016; Rajala et al. 2022; Ren et al. 2023; Yang et al. 2014; Zhang et al. 2022).

Due to differences in the oxidation process of aluminum (Berzins et al. 1977; MacLeod 1983), as well as the physio-surface properties (e.g. smoothness, biological toxicity) that promote the attachment and growth of certain microbes (Anderson and Underwood 1994; Kamimura and Araki 1984; Pearce and Chang 1982; Robert 1995), aluminum biofilms are expected to yield a taxonomic composition that is markedly different. For instance, biocorroding Zetaproteobacteria, who have been linked to the MIC of steel (Dang et al. 2011; Emerson 2018; Lee et al. 2013; McAllister et al. 2011; McBeth et al. 2011), are unlikely to be present within iron-deficient biofilms formed on aluminum surfaces. Turning to the corpus of research that exists for submerged aluminum may provide a baseline expectation for the microbial communities colonizing SAWSs (Bellou et al. 2012; Hoellein et al. 2014; Lee et al. 2014; Price 2020; Zhai et al. 2022; Zhang et al. 2019). At the phylum level, Proteobacteria, especially of the Alpha lineage, tend to dominate the bacterial assemblages, regardless of environment or aluminum alloy. Other relatively abundant taxa included Bacteroidetes, Firmicutes, Actinobacteria, and

Planctomycetota. Beyond these broad commonalities, however, exist significant variation in terms of taxonomic composition likely owed to the diversity of geographical locations and environments.

Site-specific variables such as depth, water temperature and movement, salinity, oxygen concentration, and nutrient levels determine the makeup of the free-living microbial communities in aquatic settings (Fortunato and Crump 2011; Fuhrman and Steele 2008; Lindh and Pinhassi 2018; Logue and Lindström 2008). These planktonic assemblages are often the source of colonizers for submerged surfaces, including aluminum, in the marine environment, and thus, a primary influence on biofilm composition (Dang and Lovell 2000; Dang et al. 2008; Decho 2000; Caruso 2020; Pollett et al. 2018). For example, Alphaproteobacteria dominated the shallow waters of Hongtang Bay (China), while Gammaproteobacteria were more abundant in the deep waters of Yap Trench (Zhai et al. 2022; Zhang et al. 2019). This difference was reflected in the biofilm communities formed on aluminum (commercially-pure, Al 1060) immersed in the respective environments. Contributions of the ambient seawater to surface-attached biofilms were also observed by Lee et al. (2014) when comparing bacterial colonization of aluminum from both inside and outside a cold seep brine pool. Similarly, Price (2020) found that higher environmental microbial biodiversity was linked to higher aluminum biofilm biodiversity, with salinity and water temperature driving the variation in community composition. Such examples indicate that biofilms on submerged aluminum surfaces likely possess different specialized microbial communities adapted for specific environments.

Returning to the realm of historic preservation, the impact of the surrounding sediment microbiome should not be discounted. Price et al. (2021a) noted a sediment influence on drilled shipcores from below the sediment line, including increased abundances of Deltaproteobacteria.

Similarly, while controlling for substrate-induced differences, Mugge et al. (2019a) attributed the variation in coupon biofilm communities associated with shipwrecks in the GOM to a site's proximity to the *Deepwater Horizon* oil spill footprint. The correlation of sites within the affected area and an increased abundance of hydrocarbon degraders suggested that residual oil was likely harbored within the surrounding sediment. An analysis of the sedimentary microbiomes further substantiated the conclusion that the seafloor served as the inoculum for deepwater biofilms in the GOM. These taxonomic differences had serious site preservation implications, as increased abundances of hydrocarbon-degrading bacteria corresponded with high metal loss for coupons within the spill's footprint. This suggested that MIC likely contributed to the documented, post-spill deterioration of the *U-166* (WWII German U-Boat) wreck (Damour et al. 2019).

The observed differences in community composition, despite being formed on the same substrates, demonstrates the impact the surrounding environment can have on the selection of biofilm microbes through species sorting (Basili et al. 2020; Dang and Lovell 2016; Jones et al. 2007; Lawes et al. 2016; Rao 2010). This process, which has been defined as "when bacteria are selected from a pool of species to form a community due to selection by local abiotic and biotic environmental conditions" (Zhang et al. 2014:1), has long been considered a major factor in the formation of aquatic biofilms (Besemer et al. 2007; 2012). Thus, consideration of the "background" microbiome (Hamdan et al. 2021:2889), as well as the environmental influences that shape it are especially relevant to a subject as globally distributed as WWII-era SAWSs. Using four such sites off the coast of Hawai‘i as a starting point, this article presents the first investigation into the taxonomic composition of SAWS microbiomes. While foundational in nature, the current study seeks to go beyond a 'fact-finding' examination of previously unexplored microbiomes. Instead, expected results are informed by past research related to marine biofilm, the bacterial colonization of aluminum, and the environment's filtering effect on attached microbial communities.

1) The taxonomic composition of the SAWS biofilms are hypothesized to share significant similarities with previous investigations of submerged aluminum, specifically a predominance of Proteobacteria and Bacteroidetes.

2) The influence of the surrounding environment and its microbiome are hypothesized to manifest itself within the SAWS biofilms, as evidenced by taxonomic comparisons with *in situ* sediment and seawater samples, as well as marine biofilm studies from other Hawaiian contexts. Thus, the overall marine microbiota associated with the four SAWSs is predicted to be a combined outcome of identifiable substrate and environmentally-induced variation.

3) On a more fine-scale approach to the environmental context, interisland (i.e. Maui and O‘ahu) taxonomic differences are also anticipated due to the biogeographic influence on microbiomes. Communities associated with the two Maui sites are expected to display similar microbial abundances distinguishable from those of the two O‘ahu sites, and vice versa. Specifically, the microbiomes are hypothesized to reflect the difference in anthropogenic pollution between Maui and the more urbanized O‘ahu (Hawai‘i State Department of Health 2018; Swarzenski et al. 2013).

4) Finally, given that the potential of MIC is of primary concern, biofilm sampling efforts targeted surfaces that were visibly corroded, as well as those that appeared uncorroded. Similar to the findings of Price et al. (2021), corroded sampling locations are hypothesized to yield higher abundances of microbes linked to MIC, specifically sulfate-reducing bacteria (SRB) (Hamilton 1985; Iverson, 1966; Postgate, 1979).

Using 16s rRNA gene amplicon sequencing, the microbiomes of each wreck's biofilm and the surrounding environment (i.e. sediment and seawater) were taxonomically defined and compared using various parametric and non-parametric statistical analyses. The results constitute a necessary first step in discerning the microbial communities associated with SAWSs and assessing the potential for MIC. The research presented here should not be conceived as a definitive characterization of SAWS microbiomes, but instead, serve as a comparison for geographical and longitudinal follow-up studies. The ecological data may eventually be combined with electrochemical corrosion surveys and photogrammetric documentation to track site changes and develop scientifically-informed site preservation strategies. For now, establishing a baseline is imperative due to the ephemeral nature of biofilms, as it relates to both short-term processes of formation, growth, and dispersal (Antunes et al. 2019; Landini et al. 2010; McDougald et al. 2012), and long-term climate change (Allen et al. 2021; Baragi and Anil 2016; Das and Mangwani 2015; Qian et al. 2022; Russell et al. 2013; Tuck et al. 2022; Ugya 2023).

Materials and Methods

Study Area

The Hawai‘i Submerged Cultural Resource Inventory (National Oceanic and Atmospheric Administration [NOAA] 2017) lists a total of 48 underwater aircraft wrecks in the Main Eight islands with confirmed locations. From this database, four WWII-era aircraft were chosen for microbiological sampling. Each wreck had been previously documented (Bush 2023; NOAA 2011; Petrey et al. 2008), which aided in project planning and sample recording. Sites were divided evenly between the islands of Maui and O‘ahu (Figure 4.1). The Maui wrecks, a Curtiss SB2C-1C Helldiver (Burean Number: 18400) and a suspected Grumman F6F-3 Hellcat (currently unidentified), are both located within the south-facing Māʻalaea Bay. Near eastern Oʻahu, a Republic P-47 Thunderbolt (Serial Number: 43-25601) and a suspected Goodyear FG-1A Corsair (Bureau Number: 14151, *pending confirmation*), are situated at opposite ends of Waimānalo Bay. Site descriptions are summarized below (Table 4.1). All sites are within 3 kilometers (km) of the shore and fall within depths of 4-20 meters (m), with water temperatures ranging from 25.0 – 27.2°C (Table 4.2). The Helldiver and Thunderbolt wrecks are both prominently featured as dive and snorkel tourism sites, while the Hellcat occasionally receives recreational visitors. The Corsair is in an area prone to strong currents and thus not frequented by recreational divers.

Table 4.1. Study Site Descriptions

Wreck Site	Island	Depth	Distance from Shore	Site Description	Environmental Context	Samples Collected
Curtiss SB2C-1C Helldiver	Maui	20 m	2.9 km	Nearly complete	Sandy seafloor; coral growth on wreck and significant marine life	Biofilm: 10 Sediment: 5 Seawater: 3
Grumman F6F-3 Hellcat	Maui	11 m	0.68 km	Two sections: fuselage and nose[a]	Sandy seafloor with pockets of seagrass; coral on wreck and significant marine life	Biofilm: 12 Sediment: 5 Seawater: 3
Republic P-47 Thunderbolt	Oʻahu	4 m	0.73 km	Split in two sections: fuselage and nose[b]	Extensive reef flat with pockets of sand; limited growth on wreck	Biofilm: 11 Sediment: 4 Seawater: 3
Goodyear FG-1A Corsair	Oʻahu	10 m	0.65 km	Badly disarticulated, scattered debris	Sandy seafloor with pockets of exposed bedrock and isolated reef structures; coral growth concentrated on one end of wing	Biofilm: 9 Sediment: 4 Seawater: 3

a: Sampling focused only on fuselage section
b: Sampling focused on both fuselage and nose sections
c: Sampling focused only on port wing segment

Sample Collection and Processing

A total of 73 samples (42 biofilm, 19 sediments, and 12 seawater) were collected from the four wreck sites in April and August 2021. Marine biofilm was collected from the aluminum aircraft surfaces by pairs of SCUBA divers. One of the divers would place a 10 × 10 centimeter (cm) sampling square at the desired location and use a polypropylene spatula to dislodge the biofilm material within the square. The other diver would collect the biofilm by extracting a sterilized 60 milliliter (mL) plastic syringe fitted with a 1 cm tubing attachment near the working spatula. Three syringes were used per sampling square, with sampling locations divided evenly between surfaces with and without visible corrosion (Figure 4.2). Time permitted for an additional two biofilm samples to be collected from non-aluminum surfaces (tire rubber and stainless steel) at the Hellcat site. On shore, the biofilm contents of syringes from the same sampling point were combined into a single 50 mL falcon tube and allowed to settle. The seawater supernatant was removed using serological pipettes, before sample tubes were sealed and frozen. All sampling locations were recorded on previously-constructed site plans and sample information, including depth and corrosion status, noted on underwater recording sheets. With the exception of the Corsair site, 3-dimensional (3D) photogrammetric models were generated for each aircraft with sampling locations indicated. The water column's temperature (°C) and dissolved oxygen (percent air-saturation) at each site were measured in 2 m increments using a using a YSI device (EcoSense DO200A Dissolved Oxygen Meter).

At each site, a minimum of four sediment samples (near corroded surface, near non-corroded surface, 5 m away, and 30 m away) were collected using 50 mL falcon tubes. An additional two sediment samples were collected in Maui, with one from underneath the

Helldiver’s fuselage and one from an algae-covered sand patch at the Hellcat site. Three 1 liter samples of seawater were collected from above each site in sterile Nalgene containers.

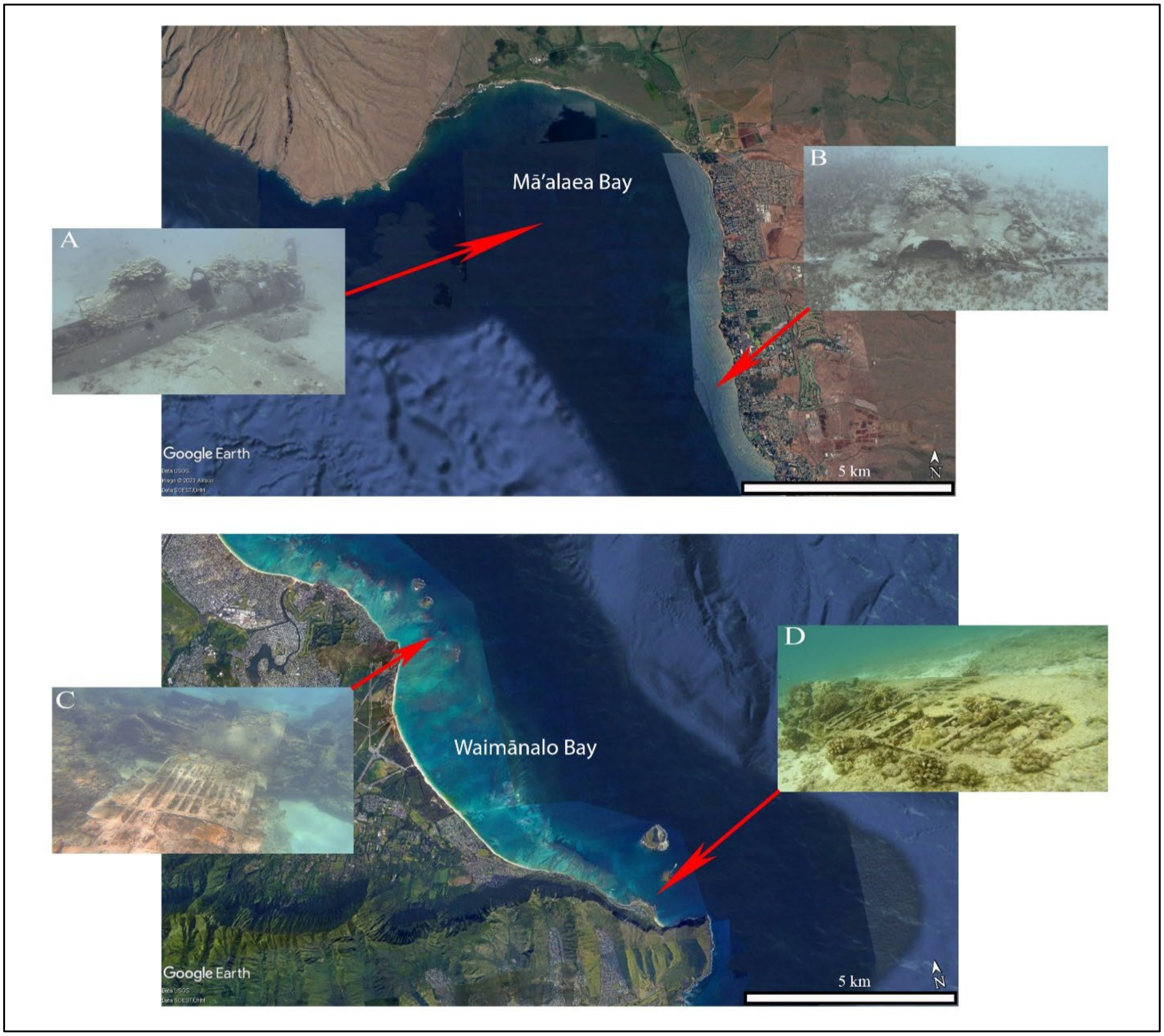

Figure 4.1. Map of Study Sites: A) SB2C-1C Helldiver; B) F6F-3 Hellcat; C) P-47 Thunderbolt; D) FG-1A Corsair. Satellite imagery courtesy of Google Earth. Site photos courtesy of East Carolina University, 2021 and Naval Exploration Research Divers, 2019.

Seawater samples were processed by placing a 0.2 µm Polyethersulfone filter into an aseptic plastic holder, before filtering (between 550-800 mL) until significant resistance was met. Each filter was then aseptically transferred to a 50 mL falcon tube. All sample tubes were sealed and kept frozen, prior to being shipped on ice from Hawaiʻi to East Carolina University

(Greenville, North Carolina). Upon their delivery in an airtight cooler, samples were immediately stored at -80°C until DNA extractions.

DNA Extraction and Sequencing

Genetic material was extracted from all biofilm and sediment samples using the MoBio DNeasy PowerSoil Kit (Qiagen, Inc.) protocol, while the DNeasy PowerWater Kit (Qiagen, Inc.) was used for seawater samples. The PowerSoil kit obtained higher DNA yields from the samples when compared to the DNeasy PowerBiofilm kit and allowed for consistent methodology between biofilm and sediment samples. All samples (n=73) met the minimum requirement for sequencing of 1 ng/µL. DNA was sent to Dalhousie University Integrated Microbiome Resource (IMR; imr.bio) for 16S rRNA gene amplicon sequencing targeting the V4-V5 region. At IMR, 16S amplicons were generated utilizing primer sets 515F+926R. Amplicon samples were then sequenced on an Illumina MiSeq using 2 × 300 bp PE v3 chemistry, which enabled paired amplicon reads to be joined into a single, high-quality read (Comeau et al. 2017). Sequence reads for every sample, except one (Thunderbolt, biofilm from non-corroded surface), were successfully returned as fastq files for downstream analyses.

Table 4.2. Water Column Data from Maui and O‘ahu

Site	Island	Temperature	Dissolved Oxygen (%)	Date of Measurement
Hellcat	Maui	25.0-25.2	85.68 ± 1.64	26 April 2021
Helldiver	Maui	25.0-25.3	91.20 ± 1.08	28 April 2021
Corsair	O‘ahu	26.2-26.3	91.83 ± 2.95	8 August 2021
Thunderbolt*	O‘ahu	27.1-27.2	90.55 ± 1.44	15 August 2021

*Note that depth at this site is limited to 4 m. All other sites were measured to 10.5 m below surface.

Microbial Community Composition & Diversity Analyses

Sequences were analyzed following the protocol by Kozich et al. (2013) using mothur v.1.48 and associated curation pipeline. Briefly, paired-end reads were merged and quality filtered, including the removal of chimera sequences. Nucleotide sequences that read at a similarity threshold (97%) for the designated marker gene (16S rRNA) were clustered into a single operational taxonomic unit (OTU). Sample OTUs were then identified taxonomically by comparing sample sequences with reference examples in the silva v.132 database. This microbial directory is the most used and most current in terms of available reference sequences and taxonomic classifications. Bacterial OTUs were identified down to the lowest taxonomic rank possible, ranging from 'unclassified bacteria' (phylum) to the genus level.

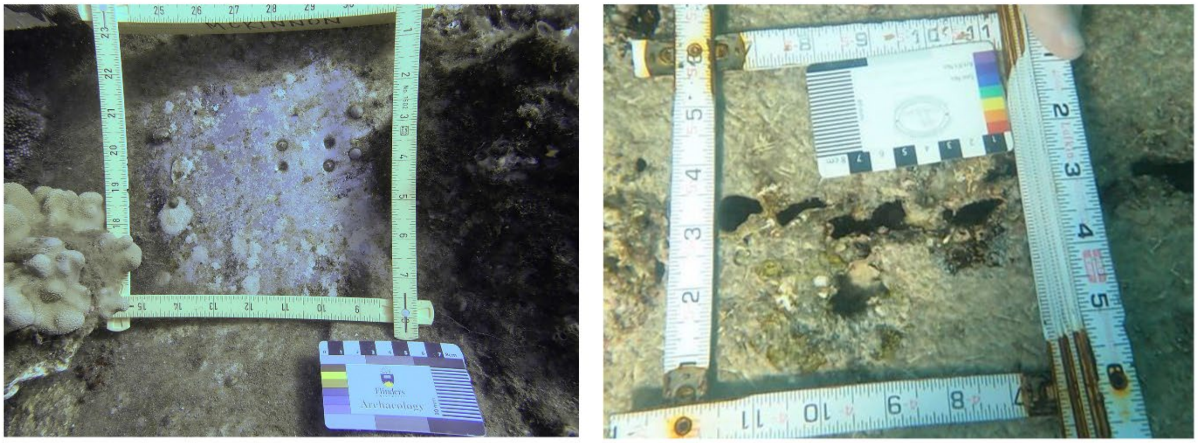

Figure 4.2. Examples of sampling surfaces. Left: non-corroded aluminum surface (Hellcat Site, Maui). Right: corroded aluminum surface (Thunderbolt Site, O'ahu). Photos courtesy of East Carolina University, 2021.

Relative abundance calculations were performed for each sample, including the relative contribution of microbes identified by Muyzer and Stams (2008) as 'sulfate-reducing bacteria' (SRB). The multivariate dataset was then subjected to non-metric multidimensional scaling (NMDS) in R using the metaMDS function with Bray-Curtis dissimilarity method (vegan package 2.6-4). The reduced dimensionality was expressed as NMDS plots (ggplot2 package). In R, the ANOSIM function (vegan) was used to evaluate the statistical differences in taxonomic composition between the microbial communities of sample groups, while the SIMPER function (vegan) was used to identify the contribution of each taxon to the average intergroup Bray-Curtis dissimilarity. Finally, community statistics, including species richness, Shannon diversity index (H'), and evenness (J) were calculated using the vegan package in R.

Results

Aluminum Biofilm

A total of 1,903,715 sequences were identified across the 41 aluminum biofilm samples, with 13,389 OTUs represented within the Maui dataset (n=20) and 23,188 OTUs within the O‘ahu dataset (n=19). Sequences identified as chloroplasts were removed. These samples, regardless of site, were dominated at the class level by Alphaproteobacteria (26.2%) and Planctomycetacia (25.0%), which made up over half of the total assemblage. Cyanobacteria (10.0%), Flavobacteriia (9.6%), and Gammaproteobacteria (8.1%) were the next three most abundant taxa.

For each island, OTU presence and absence were calculated, with OTUs that appeared in at least 75% of biofilm samples (O‘ahu: 15/20; Maui: 15/19) being used to infer a ‘core’ biofilm microbiome. This resulted in the selection of 515 OTUs from the two Maui sites (Hellcat and Helldiver), which accounted for 68.3% of sequences, and 1149 OTUs (72.9% of sequences) for the O‘ahu (Corsair and Thunderbolt) sites. The core microbial community for both islands mainly consisted of OTUs from the Planctomycetacia (Maui: 27.0%, O‘ahu: 23.8%), Alphaproteobacteria (Maui: 16.5%, O‘ahu: 17.1%), Gammaproteobacteria (Maui: 16.1%, O‘ahu: 10.7%), and Flavobacteriia (Maui: 9.3%, O‘ahu: 5.9%) classes. For the Maui sites, 163 OTUs (42.6% of sequences) were ubiquitous (identified within 100%) to the biofilm samples, while the O‘ahu biofilm assemblage possessed 359 ubiquitous OTUs (52.1% of sequences). Again, OTUs primarily belonged to the Planctomycetacia (Maui: 29.4%, O‘ahu: 29.5%), Alphaproteobacteria

(Maui: 22.1%, O‘ahu: 18.9%), Gammaproteobacteria (Maui: 20.9%, O‘ahu: 15.6%), and Flavobacteriia (Maui: 9.8%, O‘ahu: 7.8%) classes.

An initial visual inspection of the NMDS plot generated using the aluminum biofilm taxonomic data suggested that sample biogeography was a primary influence on the biofilm communities (Figure 4.3). The results indicate that biofilm samples associated with Maui and O‘ahu, respectively, are significantly different from one another in terms of taxonomic composition. This interpretation was empirically supported by the results of the ANOSIM test (island, $R = 0.7034$, $p = 0.0001$). According to the SIMPER analysis, Planctomycetacia (26.4%), Alphaproteobacteria (25.6%) Cyanobacteria (10.7%), Gammaproteobacteria (9.1%), and Flavobacteriia (7.4%) contributed the most to the taxonomic differences between the Maui and O‘ahu biofilms. Of these, only Planctomycetacia is more relatively abundant amongst O‘ahu (26.0%) samples when compared to those from Maui (20.4%). The other four bacterial classes each comprised a larger percentage of the Maui dataset as compared to that of O‘ahu.

Based on the patterning of the NMDS plot, the interisland differences are far less apparent when only considering Dimension 1. The ANOSIM tests were repeated by pairing the O‘ahu Corsair and Maui Hellcat together and comparing their assemblages against those of the O‘ahu Thunderbolt and Maui Helldiver. The new grouping (Helldiver-Thunderbolt and Hellcat-Corsair) resulted in a near significant result ($R = .0756$, $p = .055$). To further explore these intra-island differences between wreck biofilm samples, separate NMDS models were constructed for each of the islands, thus enabling comparisons between both the Hellcat and Helldiver sites, as well as the Corsair and Thunderbolts sites. The ANOSIM test was found to be significant for Maui ($R = 0.1838$, $p = 0.0254$) and nearly significant for O‘ahu ($R = 0.1402$, $p = 0.0574$).

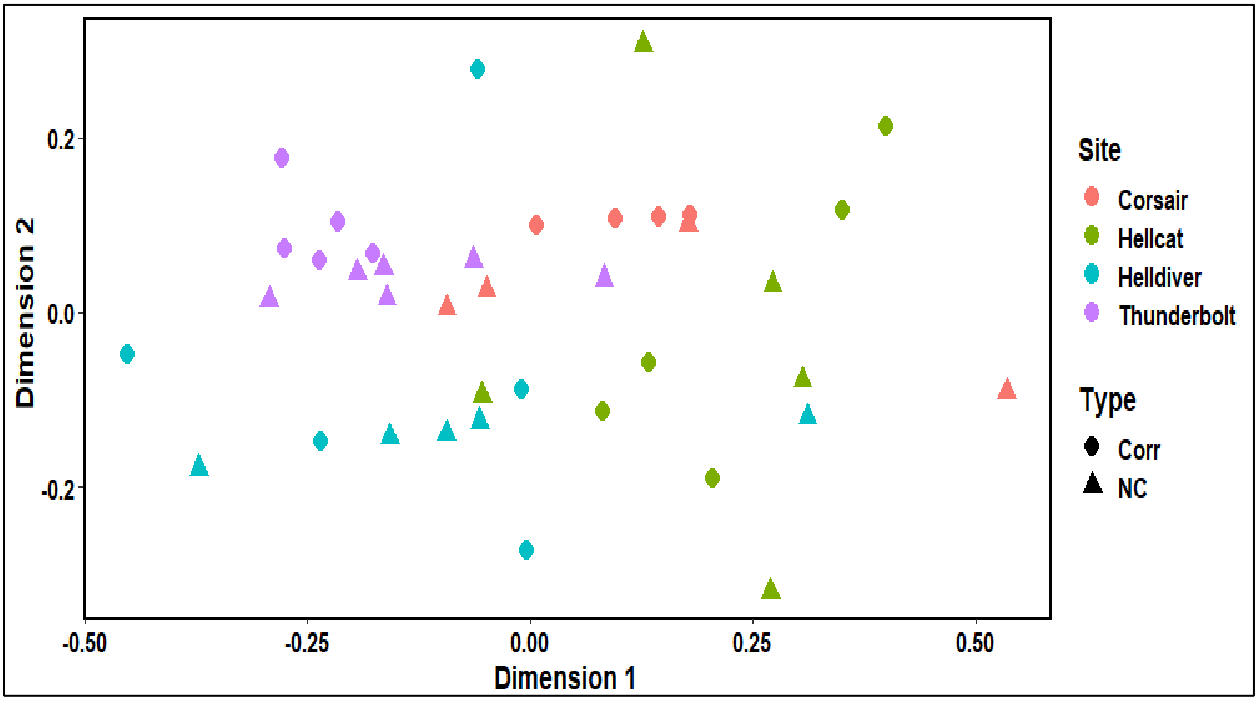

Figure 4.3. Non-metric multidimensional scaling plot for all aluminum biofilm samples. Stress = 0.1679621. NC = Non-Corroded wreck surface. Corr = Corroded wreck.

In Maui, differences in taxonomic composition amongst the Hellcat and Helldiver biofilms are attributed to Alphaproteobacteria (25.1%), Cyanobacteria (17.9%), Planctomycetacia (17.6%), Flavobacteriia (9.3%), and Gammaproteobacteria (8.7%) (Figure 4.4). While Alphaproteobacteria and Planctomycetacia rank first and second in terms of relative abundance at both sites, the contribution of each of these taxa is nearly equal at the Hellcat site (Alphaproteobacteria: 25.1%, Planctomycetacia: 25.0%), whereas Alphaproteobacteria (27.6%) are far more dominant than Planctomycetacia (17.1%) at the Helldiver site. Flavobacteriia and Cyanobacteria are also more relatively abundant at the deeper Helldiver site (10.7%, 16.7%), as compared to the Hellcat site (8.2%, 3.8%). Gammaproteobacteria, Unclassified Bacteria, Deltaproteobacteria, and Acidobacteria, on the other hand are relatively more abundant within the Hellcat biofilm (21.2%) than the Helldiver (16.2%).

A somewhat similar pattern is observed for comparisons amongst the biofilm from Oʻahu sites (Figure 4.4). The SIMPER analysis revealed that the same five taxa Alphaproteobacteria (23.8%), Planctomycetacia (21.6%), Cyanobacteria (15.8%), Flavobacteriia (8.3%), and Gammaproteobacteria (8.1%), contributed the most to inter-site differences between the Corsair and Thunderbolt. Like the Helldiver site on Maui, the Thunderbolt site's microbiome is dominated by Alphaproteobacteria (27.2%), Planctomycetacia (24.9%), and Cyanobacteria (12.4%), with a relatively high abundance of Flavobcateriia (8.7%). The microbial communities associated with the Corsair site are defined by a higher abundance of Planctomycetacia (27.9%), as opposed to Alphaproteobacteria (23.9%). Additionally, Gammaproteobacteria, Unclassified Bacteria, Deltaproteobacteria, and Acidobacteria were each more at the Corsair site than the Thunderbolt, comprising 25.1% of the former and only 15.4% of the latter.

The ecological community statistics added further context to the patterns observed within the structure of the dataset, particularly as it relates to the unexpected similarities between sites from different islands (i.e. Corsair and Hellcat; Thunderbolt and Helldiver) (Table 4.3). The Corsair site averaged the highest level of bacterial family richness (n=205.1), while the Helldiver site yielded the lowest average richness value (n=162.0). The Hellcat site was only slightly less rich on average (n=179.3) than the Thunderbolt site (183.0). The Hellcat wreck's microbiome was the most diverse (H=3.63) and evenly distributed (E=1.61), while the Corsair site ranked second in terms of both (H=3.52, E=1.53). Both the Helldiver (H= 3.32, E=1.51) and Thunderbolt (H=3.34, E=1.48) had similarly low levels of diversity and evenness, suggesting that these two sites are most dominated by a limited number of taxa.

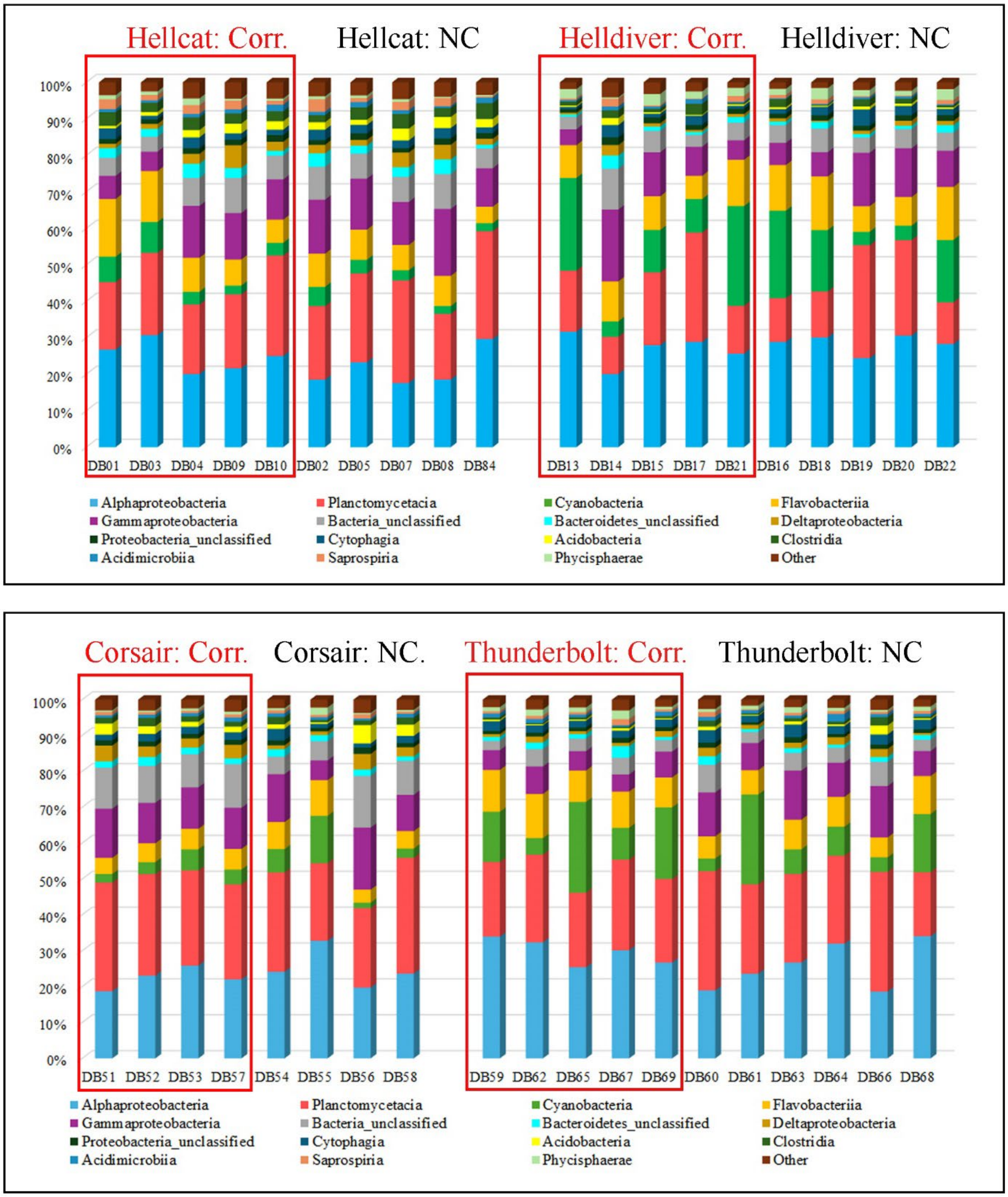

Figure 4.4. Relative abundance for aluminum biofilm samples from Maui (top) and O‘ahu (bottom). NC = Non-Corroded wreck surface. Corr = Corroded wreck surface.

Microbiologically-Influenced Corrosion

Despite the observed differences between the individual sites, there were no significant differences between the microbial community composition of all biofilm samples collected from visibly corroded wreck surfaces. Three of the sites, Helldiver (*R* = -0.084, p = 0.6601), Corsair (*R* = -0.03125, p = 0.4866), and Thunderbolt (*R* = -0.08267, p = 0.7498), produced a negative ANOSIM test value, while the Hellcat site yielded a slightly positive value (R = 0.012, p = 0.4135). While at the class level, there appears to be no appreciable differences in the overall microbiomes composition at the class level of samples from corroded and non-corroded wreck surfaces, there were notable contrasts as it relates to sulfate-reducing bacteria (SRB), a key contributor to MIC process.

Table 4.3. Richness, Diversity (H'), and Evenness (J) Measurements for Aluminum Biofilm Samples

Site	Sample Type	Samples	Richness	Diversity (H')	Evenness (J)	Sequences
Hellcat	Corroded	5	189.6 ± 20.7	3.67 ± 0.09	1.62 ± 0.07	95,986
Hellcat	Non-Corroded	5	169.0 ± 6.5	3.59 ± 0.20	1.61 ± 0.09	50,978
Corsair	Corroded	4	215.0 ± 16.4	3.58 ± 0.03	1.54 ± 0.02	276,759
Corsair	Non-Corroded	4	195.3 ± 25.5	3.47 ± 0.06	1.52 ± 0.03	274,655
Helldiver	Corroded	5	152.4 ± 15.8	3.29 ± 0.05	1.51 ± 0.05	75,023
Helldiver	Non-Corroded	5	171.6 ± 25.7	3.35 ± 0.19	1.50 ± 0.07	121,128
Thunderbolt	Corroded	5	178.8 ± 10.9	3.31 ± 0.09	1.47 ± 0.05	448,466
Thunderbolt	Non-Corroded	6	186.5 ± 24.7	3.37 ± 0.16	1.49 ± 0.05	573,666

One standard deviation (±). Richness calculated at the Family level.

Using the phylogenetic tree of SRB in Muyzer and Stams (2008), a total of 24 taxa classified as sulfate-reducing bacteria were identified within the overall dataset, representing 16 genera, 6 families, and 4 orders. All SRB were from the Deltaproteobacteria class. The SRB relative abundance across each sample type was calculated and compared with the maximum

SRB relative abundance yielded by an individual sample for that type (Figure 4.5). Though the Hellcat site biofilm possesses the highest percentage of SRB sequences (1.61%), the Helldiver site ranks last in terms of SRB abundance within biofilm samples (0.41%). Biofilm from the Corsair site yielded the second highest contribution of SRB (0.83%), while the Thunderbolt site (0.54%) was more similar to the Helldiver. The Corsair site is also the only one of the four that demonstrates an appreciable difference between corroded (1.18%) and non-corroded locations (0.49%). For the remaining three sites, differences in average SRB abundance between corroded and non-corroded locations is negligible. The *Desulfobulbaceae* family are the primary SRB taxa for the vast majority (92.9%) of biofilm samples from the Hellcat, Helldiver, and Corsair sites. Samples from the Thunderbolt site diverge slightly from this pattern, with 6 samples, including all 5 from corroded locations, having an SRB assemblage primarily made up of bacteria from the *Desulfovibrionaceae* family. The remaining five biofilm samples mirror that of the other wrecks with a preponderance of *Desulfobulbaceae* bacteria.

Comparisons to Non-Aluminum Biofilm

Given that only two non-aluminum biofilm samples (one steel, one tire rubber) were sequenced, it is impossible to perform meaningful statistical tests between communities associated with these materials and those linked to aluminum surfaces. There are, however, several obvious differences between the taxonomic composition of these non-aluminum biofilms and that associated with aluminum. Unclassified Bacteria ranked first in relative abundance for both steel (32.1%) and tire rubber (17.5%), with a relatively low abundance of Planctomycetacia (steel: 5.4%, tire rubber: 11.2%) and Alphaproteobacteria (steel: 11.7%, tire rubber: 15.9%) when compared to the aluminum biofilm samples. Both Gamma- and Deltaproteobacteria are more abundant within the steel (14.4%, 7.0%) and tire rubber (14.3%, 4.5%) than the averages for the aluminum samples (10.1%, 1.8%). Acidobacteria, though a minor component of both the steel sample (2.0%) and average aluminum sample (1.2%), were highly abundant for the rubber tire sample (7.5%) and greatly exceeded the maximum value for aluminum samples (2.7%). Finally, SRB abundance within the steel (4.6%) and tire (3.0%) samples was considerably higher than the average aluminum biofilm sample (0.8%).

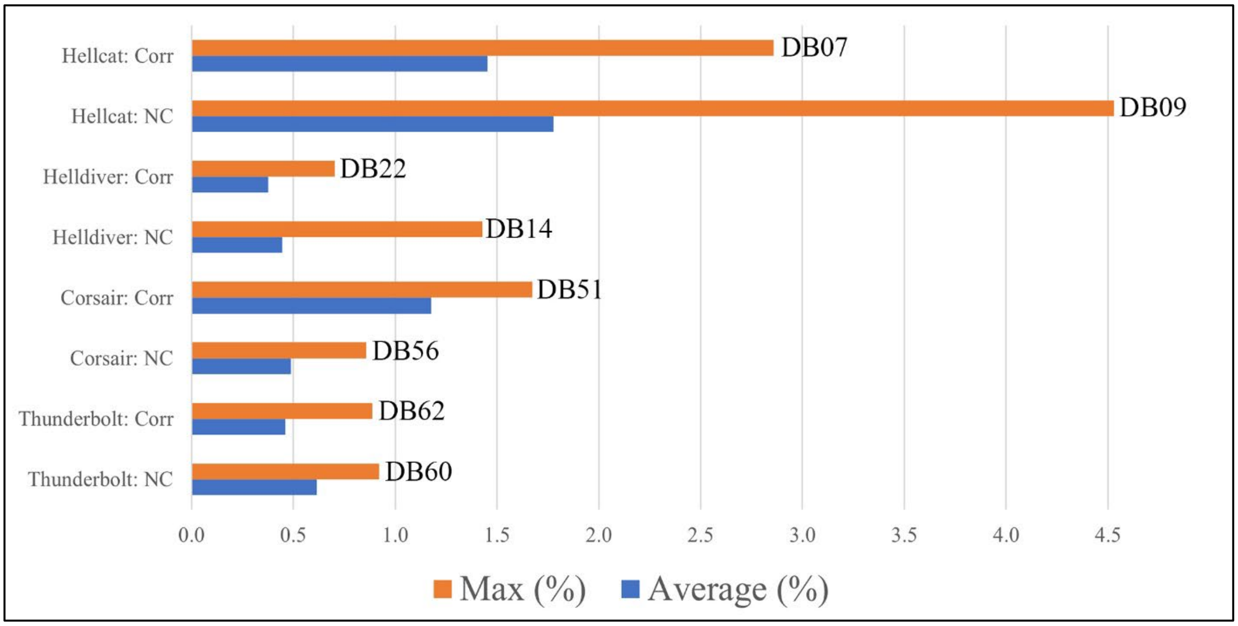

Figure 4.5. Average and maximum SRB relative abundance for corroded (Corr) and non-corroded (NC) wreck surfaces. The ID for the sample that yielded the maximum value is given.

Environmental Microbiome

Among the sediment and seawater samples, a total of 1,359,029 sequences were identified, with 18,394 OTUs represented within the Oʻahu dataset (n=14) and 15,872 OTUs within the Maui dataset (n=16). As expected, the microbiomes of the sediment and seawater are not only distinct from one another but are mostly differentiated from those of the wreck biofilms (material, $R = 0.3752$, $p = 0.0001$) (Figure 4.6). There is, however, an apparent overlap between the biofilm and sediment, indicative of taxonomic similarities shared between the two sample types. Overall, Planctomycetacia (25.8%), Gammaproteobacteria (18.6%), Unclassified Bacteria

(16.1%), Deltaproteobacteria (7.0%), Alphaproteobacteria (6.7%), and Acidobacteria (6.7%) were the most relatively abundant taxa amongst sediment samples.

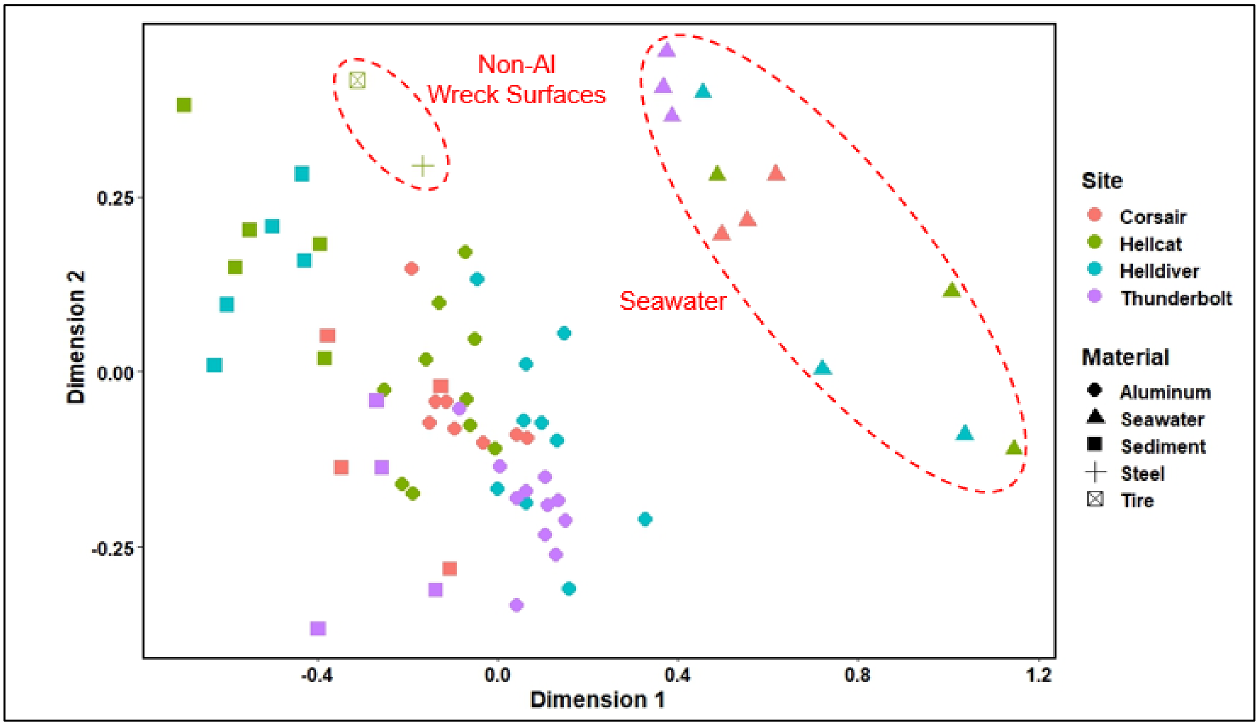

Figure 4.6. Non-metric multidimensional scaling plot for entire dataset. Stress: 0.1186. ANOSIM: material, $R = 0.3752$, $p = 0.0001$; island, $R = 0.5378$, $p = 0.0001$.

There are notable interisland differences as it pertains to sediment microbiomes (Figure 4.7). While the average species richness varied amongst the four sites (Hellcat: 196.0, Thunderbolt: 191.5, Corsair: 167, Helldiver: 160.4), Maui sediments were considerably more diverse (Hellcat: 3.57, Helldiver: 3.56) and taxonomically even (Hellcat: 1.57, Helldiver: 1.62) as compared to O‘ahu sediments. The Corsair site sediments yielded an average diversity of 3.25 and evenness of 1.47, while the Thunderbolt site sediment was the least diverse (H=3.09) and even (E=1.36). In Maui, Gammaproteobacteria and Unclassified Bacteria are the most relatively abundant in sediment samples, with nearly identical percentages of Planctomycetacia, Deltaproteobacteria, Alphaproteobacteria, and Acidobacteria (in descending order) for both sites. Sediments at both O‘ahu sites are overwhelmingly dominated by Planctomycetacia, while possessing similar abundances of Gammaproteobacteria, Unclassified Bacteria, Alphaproteobacteria, Acidobacteria, and Deltaproteobacteria (in descending order).

According to the SIMPER analysis, most of the interisland difference (35.6%) is attributed to the dominance of Planctomycetacia within O‘ahu sediments, with Gammaproteobacteria (16.6%), Unclassified Bacteria (13.3%), Acidobacteria (5.2%), Alphaproteobacteria (5.2%), and Deltaproteobacteria (5.0%), all more abundant in Maui sediments, contributing the next most to the observed variation. The relatively high abundance of Deltaproteobacteria can be further examined in terms of SRB. Significantly higher SRB abundances were observed at the Hellcat (average:8.3%, max: 10.0%) and Helldiver (average: 7.5%, max: 11.0%) site sediments, as compared to the O‘ahu Corsair (average: 0.8%, max: 2.1%) and Thunderbolt (average: 0.6%, max: 1.8%). Unlike biofilm, the SRB assemblages of sediment samples are dominated by sequences belonging to the *Desulfobacteraceae* family, as opposed to *Desulfobulbaceae*.

Seawater samples microbiomes were largely defined by the dominance of Flavobacteriia, Cyanobacteria, and Alphaproteobacteria, which accounted for 86.8% of the total seawater bacterial assemblage. Seawater samples were far less diverse (H = 2.31, SD 0.22) and taxonomically even (E = 1.12, SD 0.09) than either biofilm or sediment. The Thunderbolt site averaged the highest bacterial family richness (n=195.0), followed by the Corsair site (n=171.0). The Maui sites contained considerably less species richness (Hellcat: 65.7, Helldiver: 87.7). O‘ahu sites possessed similar levels of diversity (Corsair: 2.54, Thunderbolt: 2.50), both much higher than the Maui sites (Hellcat: 2.10, Helldiver: 2.10). Seawater samples demonstrated a relatively high level of congruity in terms of evenness between the four sites (Hellcat: 1.19, Corsair: 1.14, Helldiver and Thunderbolt: 1.09). Taxonomically, seawater samples from the Maui sites compared favorably to one another, with Flavobacteriia, Cyanobacteria, and Alphaproteobacteria (in descending order) being the most abundant taxa (Figure 4.7). Conversely, seawater samples from the O‘ahu sites, which are geographically further (7.6 km) from each other than the Maui sites (4.1 km), demonstrate less homogeneity. Seawater samples from the inshore Thunderbolt site are equally dominated by Alphaproteobacteria (35.3%) and Flavobacteriia (34.1%), whereas the Corsair site waters are primarily composed of Cyanobacteria (36.3%), with lesser contributions from Alphaproteobacteria (29.9%) and Flavobacteriia (17.2%). In sum, Maui sediments tended to be more diverse and evenly distributed, while O‘ahu waters were considerably richer and diverse.

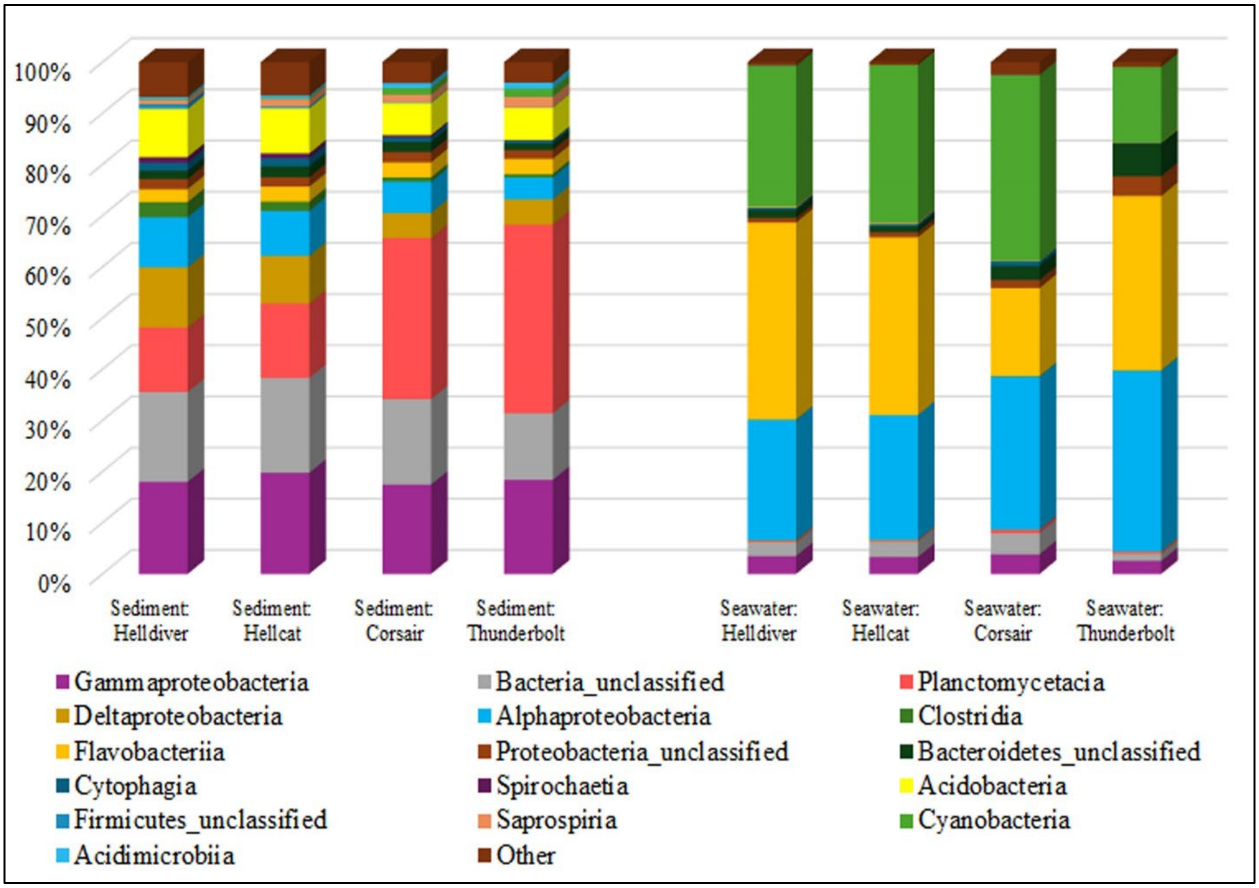

Figure 4.7. Relative abundance of environmental samples by type and site.

Unique Biofilm Taxa

The analysis of the environmental microbiome enabled the ability to better understand which microbes are unique to aluminum biofilms. Seawater and sediment samples were pooled together into an 'environmental' composite for both islands (Maui: OTUs; O'ahu: OTUs). The OTUs that were completely absent from the environmental aggregates were then further analyzed for prevalence across the individual aluminum biofilm samples. For Maui, this resulted in 8,008 OTUs (chloroplasts removed), which accounted for 23.8% of the total sequences within aluminum biofilm samples. Of those OTUs only identified from aluminum wreck surfaces belonging to the two Maui sites, 34 are present in at least 75% of such samples, which accounts for 7.2% of all sequences identified within aluminum biofilm samples from Maui. Three OTUs, two belonging to the Pirellulales order and one belonging to the *Verrucomicrobiaceae* family, were ubiquitous to all 20 aluminum biofilm samples from Maui, while being absent from the environment. The O'ahu dataset produced a higher total of OTUs unique to aluminum biofilm samples, with 14068 OTUs absent from the environmental aggregate for O'ahu. This accounted for 12.4% of the total sequences within O'ahu aluminum biofilm samples, with 77 OTUs present in at least 75% such samples (1.6% of sequences). A single OTU, also from the Pirellulales order, represented the lone taxon ubiquitous to all 19 aluminum biofilm samples from O'ahu. An additional 5 OTUs (2 Rhodospirillales, 1 Pirellulales, 1 unclassified Planctomycetes, and 1 unclassified Gammaproteobacteria) were present in 18 of the 19 O'ahu biofilm samples, while remaining absent from the environment.

Interisland comparisons of the taxonomic composition for the OTUs unique to aluminum biofilm samples revealed key similarities. Of the OTUs present in at least 75% of Maui wreck samples and absent from environmental samples, 50.7% of those sequences were identified as belonging to the Cyanobacteria class, with Alphaproteobacteria (20.5%) and Planctomycetacia (11.3%) ranked second and third in terms of sequence abundance. The Oʻahu aluminum biofilms exhibited a similar pattern, as sequences belonging to the Cyanobacteria (27.4%), Alphaproteobacteria (27.2%), and Planctomycetacia (16.7%) classes were the most abundant amongst the OTUs unique to aluminum biofilm samples. Several genera and families were identified exclusively within aluminum biofilm samples. For Maui, 5 taxa were found in at least 8 of the 20 biofilm samples, while remaining absent from sediment and seawater samples. This included the genera *Wenzhouxiangella* (Gammaproteobacteria) and *Rubricoccus* (Rhodothermia), as well as two Cyanobacteria families, *Acaryochloris* and Group I. For Oʻahu, 10 taxa fit this description, including the *Zehria* family (Cyanobacteria) and *Roseovarius* (Alphaproteobacteria) genus which are present in 17 of the 19 biofilm samples. The remaining taxa include four Alphaproteobacteria genera (*Defluviicoccus, Pyruvatibacter, Albimonas, Neorickettsia*), two Cytophagia genera (*Marinoscillum* and *Tunicatimonas*), and the genera *Cryomorpha* (Flavobacteriia) and *Puniceicoccus* (Opitutae).

Discussion

Efforts to characterize the impact microorganisms have on SAWS preservation have been hindered by a lack of taxonomic data. To that end, this study succeeded in providing the first assessment of the microbial communities colonizing the surfaces of four SAWSs off Maui and Oʻahu. Relative abundancies and other measures of community composition provided insights into the structure and diversity of the bacterial populations that are currently present within the wreck sites' biofilm. Yet, of equal concern, is how these microbes are assembled into the identified communities, particularly as it relates to the selective forces and ecological relationships. The original hypotheses identified four potential drives of community composition: substrate, environmental microbiome, geographical location, and attachment site. The species sorting process owed to this combination of biotic and abiotic variables was thus an integral aspect of this study. By simultaneously considering the current biofilm communities, including the presence and absence of key taxa, and the factors responsible for biofilm formation, the conditions that potentially enable MIC are more thoroughly investigated.

While a certain level of competition undoubtedly exists within marine biofilms, cooperation, namely, the creation of microenvironmental conditions and molecular exchanges that support metabolism, renders this form of communal living as an advantageous evolutionary strategy rooted in bacterial phylogeny (Dang and Lovell 2016; De Carvalho 2018; Guillonneau et al. 2018; Luo et al. 2013; Matz et al. 2008; Nadell et al. 2008; Parrilli et al. 2022; Parsek and Greenberg 2005; Wahl et al. 2012; Wang et al. 2023). Within the ocean, the combined effects of microorganism transport facilitated by circulating seawater and the documented microbial diversity of marine sediments expose substrates and established biofilms to influxes of microbial populations (Antunes et al. 2019; Basili et al. 2020; Dang et al. 2008; Lee et al. 2014; Rajeev et al. 2019; Sushmitha et al. 2023; Wang et al. 2022; Zhang et al. 2019). Consequently, marine biofilms are diverse and dynamic systems that exhibit quantifiable progressions in community composition, which begin with the initial colonization of a substrate. As a biofilm matures, microbial cell counts and species tend to increase, reaching episodic periods of quasi-stability (Briand et al. 2022; Moss et al. 2006; Pollet et al. 2018; Qian et al. 2022; Remple et al. 2021; Tobias-Hunefeldt et al. 2021). The exact nature of this progression and community structure differs geographically, with the variables affecting marine biofilm biodiversity equally varied and often locally-dependent (Alotaibi et al. 2021; Dobretsov 2010; Flemming and Wuertz 2019; Haggerty and Dinsdale 2017; Kriwy and Uthicke 2011; Lu et al. 2023a; Oberbeckmann et al.

2014, 2016; Toyofuku et al. 2016; Tuck et al. 2022; Wimpenny 1996). Thus, biofilm taxonomic composition can be considered the amalgamation of the environmental microbiome, niche specificity, ecological associations, and a degree of stochasticity.

The microbiome associated with the aluminum aircraft wreck surfaces exhibits a taxonomy that is, indeed, both niche-specific and environmentally-influenced. The former is signified by key commonalities shared by the biofilms from the four SAWSs, which help differentiate the taxonomic makeup of these samples from those associated with sediment, seawater, and non-aluminum wreck surfaces. Inter-site differences, however, highlight the effect the surrounding environmental microbiomes and conditions have on the biofilm communities. These findings are consistent with what has been found in non-aluminum based wreck studies (Moseley et al. 2022; Mugge et al. 2019a; Mugge et al. 2023a, 2023b; Price et al. 2021a). It is important to remember, however, that the microbial community data presented represents a 'snapshot', as opposed to a conclusive characterization. Marine biofilms are taxonomically dynamic, owing to climatic changes, both seasonally and long-term, as well as the processes of biofilm maturation and dispersal (Caruso 2020; Chung et al. 2010; Dang and Lovell 2016; Lee et al. 2008; McDougald et al. 2012; Salta et al. 2013; Sauer et al. 2022; Van Mooy et al. 2014). Though wreck biofilms are then likely to yield slightly different results in subsequent sampling endeavors, there are some over-arching patterns regarding the current dataset that warrant further discussion.

Substrate Impact

The aluminum substrate served as the first hypothesized influence on the composition of SAWS biofilm communities. Specifically, it was predicted that the taxonomic data for the present study would accord with past research on aluminum biofilms in aquatic settings (Bellou et al.

2012; Hoellein et al. 2014; Lee et al. 2014; Price 2020; Zhai et al. 2022; Zhang et al. 2019). At the phylum level, for which most of the previous studies have reported the taxonomic data at, Proteobacteria are overwhelmingly the dominant taxon (Figure 4.8). Likewise, biofilm samples from each of the four duralumin (Al2024) aircraft yielded relatively high abundancies of Proteobacteria, though this phylum's contribution to the aircraft microbiome is towards the middle to lower range for aluminum biofilms. The presence of bacteria belonging to the Bacteroidetes phylum was also comparable across the aluminum substrates, including the WWII aircraft sites. Apart from these broad similarities, however, the microbiomes of the Hawaiian SAWSs diverge from those associated with other submerged aluminum substrates. The former is noted for the increased contribution of Planctomycetes and Cyanobacteria to the overall microbial assemblages. These taxa were not observed for the majority of previous aluminum biofilm studies, with the exception of Planctomycetes at Pamlico River, US (Price 2020) and the Red Sea Brine Pool (Lee et al. 2014), as well as Cyanobacteria at Hongtang Bay, China (Zhang et al. 2019). The taxonomic data presented in Figure 4.8, helps to elucidate how substrate composition can generate comparable abundances of certain bacterial phyla, while contrasts hint to the effects that additional factors have on the assembly of biofilm communities. Thus, the relatively higher proportion of Planctomycetes and Cyanobacteria in the SAWS biofilms, as well as the relative lack of Firmicutes and Actinobacteria as compared to past studies of aluminum biofilms, is likely representative of local species sorting.

Substrate influence on the SAWS biofilm communities can be further examined as it pertains specifically to Proteobacteria. Of particular interest to MIC, was the near absence of Zetaproteobacteria, which have been frequently identified within marine corroded contexts, including steel shipwreck studies (Little et al. 2019; Mugge et al. 2019a; Price et al. 2021a; Van

Landuyt et al. 2022). Zetaproteobacteria were present in only 3 of the 41 SAWS biofilm samples, with their abundance limited to three identified sequences. This omission is likely indicative of the role substrate plays in determinizing community composition and represents a key potential difference between the MIC of steel and aluminum in marine environments. While the lack of Zetaproteobacteria reveals how substrate material influences the assembly of marine microbes, the proliferation of Alphaproteobacteria does not necessarily equate to proof of this bacterial class's specific preference for aluminum.

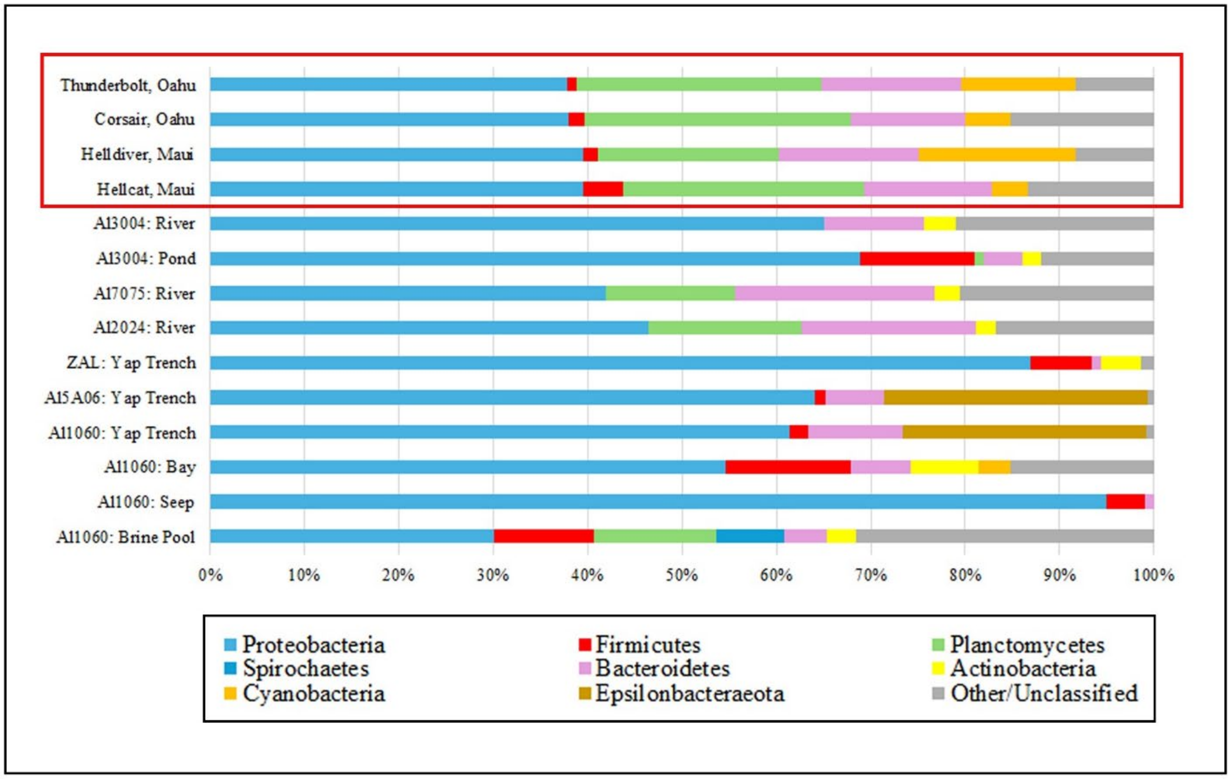

Figure 4.8. Relative abundance data at the phylum level for the Hawai'i SAWSs and previous studies of aluminum biofilms (Hoellein et al. 2014; Lee et al. 2014; Price 2020; Zhai et al. 2022; Zhang et al. 2019). Note that 'ZAL' refers to an aluminum-copper alloy. All other alloys are referred to by 'Al' and their series number. The incubation environment is listed after the alloy.

Rather, Alphaproteobacteria appear well-suited for attached-living strategies, often irrespective of substrate material. Alphaproteobacteria are abundant throughout the world's oceans (Sunagawa et al. 2015), with studies confirming their preponderance in marine biofilms

(Dang et al. 2008; Muthukrishnan et al. 2019; Papadatou et al. 2021; Tan et al. 2015; Wang et al. 2022). This appears especially true for artificial surfaces in coastal locales, where heterotrophic Alphaproteobacteria form ecological associations with autotrophs that thrive in shallower waters (Chung et al. 2010; Dang and Lovell 2000; Fischer et al. 2014; Mohamed et al. 2023; Rampadarath et al. 2017).

The majority of Alphaproteobacteria identified within the SAWS biofilm samples belong to the *Rhodobacteraceae* family, which possess a suite of physiological and genetic traits that facilitate surface living (Dang and Lovell 2002; Simon et al. 2017; Slightom and Buchan 2009). This group was previously documented as the dominant constituent of biofilms formed in Oʻahu waters (Lema et al. 2019; Vijayan and Hadfield 2020). *Rhodobacteraceae*, much like the overall Alphaproteobacteria class, is a highly diverse family and likely plays a multi-faceted role in shaping the community composition of marine biofilms (Dang and Lovell 2016; Elifantz et al. 2013; Henriksen et al. 2022; Kviatkovski and Minz 2015). For the current study, Alphaproteobacteria also constituted a significant portion of the microbial communities associated with seawater at each of the four SAWSs (average relative abundance: 28.3% ± 4.7%). By comparison, this bacterial class serves as a minor component of the sedimentary assemblages (7.2% ± 2.2%). Thus, it appears that the wrecks operate as attachment sites for free-floating Alphaproteobacteria, who can take advantage of communal living and further contribute to biofilm development through the secretion of adhesive substances (Kviatkovski and Minz 2015; Llamas et al. 2010).

The Alphaproteobacteria example and comparisons with biofilm communities associated with various aluminum substrates demonstrate the overarching takeaway as it pertains to substrate impact. The physiochemical makeup of a submerged surface, including its metallurgic and molecular properties, are a less pronounced influence on the marine biofilm communities. Instead, the simple presence of a substrate for microbial colonization encourages a form of symbiotic, attached living that promotes the growth of biofilm constituents commonly observed in marine contexts. Sushmitha et al. (2021:15) arrived at a similar conclusion in their study of marine biofilms, finding that their results "refuted the presumption that substrate material has a major impact…rather, the effect of substrate material was overwhelmed by temporal succession and in situ environmental conditions." These interpretations echoed the earlier work of Hoellein et al. (2014), who compared the biofilm communities associated with anthropogenic litter, including aluminum (Al3004), and organic substrates (e.g. cardboard and leaves). The authors of that study observed few taxonomic differences between the biofilms formed on the litter pieces (glass, plastic, aluminum, and tile), with these communities only being distinct from the cellulose-degrading assemblages formed on the organic materials. Additionally, Hoellein et al. (2014) concluded that the incubation environment (e.g. river, pond, or artificial stream), rather than substrate, dictated the composition of microbial biofilms. Thus, the identifiable effect of substrate, as reported by Mugge et al. (2023a, 2023b), is likely more apparent when comparing substrates of considerably different composition (e.g. wood and metal), or examining rare community members, such as Zetaproteobacteria.

Environmental Influence

The second hypothesized driver of biofilm community composition was the ambient environment, specifically the microbiomes of the sediment and seawater. It was anticipated that the local consortia of free-floating and sedimentary microbes would serve as the populations for biofilm communities to select from, which would result in identifiable similarities between wreck and environmental datasets. Beyond the abundance of Alphaproteobacteria in the

Hawaiian seawater and the corresponding inclusion in SAWS biofilms, the integration of free-floating communities into the biofilms at all four sites extended to Flavobacteriia and Cyanobacteria, who were amongst the five most abundant classes. Cyanobacteria, along with Alphaproteobacteria, are often the dominant bacterial types in Hawaiʻi's oligotrophic waters (Apprill and Rappe 2011; Brandon 2006; Chamberlain et al. 2014). This was observed for the Oʻahu water samples, though Flavobacteriia ranked first for Maui seawater samples, followed by Cyanobacteria and Alphaproteobacteria. With respect to the Māʻalaea Bay (Maui) waters, the higher proportion of Flavobacteriia to Cyanobacteria and Alphaproteobacteria may suggest that these waters are more eutrophic, contrary to expectations regarding the more urbanized Oʻahu. Remple et al. (2021:84) found that with "increased nutrients, populations of bacteria typically associated with oligotrophic coral reefs decreased, including groups of Alphaproteobacteria and Cyanobacteria and shifted toward populations of copiotrophic Flavobacteriia." The latter is also frequently correlated with phytoplankton blooms (Buchan et al. 2014), which are known to seasonally fluctuate in Hawaiʻi, corresponding to changes in sunlight, nitrogen fixation, and upwelling (Friedrich et al. 2021).

Regardless of this difference, the integration of Flavobacteriia and Cyanobacteria into the wreck biofilm communities is likely owed to seawater serving as an inoculum. Flavobacteriia are frequently observed as members of bacterioplankton communities, as was the case for the Hawaiian seawater samples, leading to their widespread abundance in marine biofilms (Pollet et al. 2018). There, Flavobacteriia are known to be efficient degraders of complex organic materials (e.g. polysaccharides) and form associations with algae, similar to Alphaproteobacteria (Kirchmann 2002; Mann et al. 2013; Thomas et al. 2021; Williams et al. 2013). As nutrient cyclers, Flavobacteriia are responsible for producing some of the organic waste utilized as terminal electron donors by other microbes within biofilms and thus, considered “a keystone bacterial group in the formation and functioning of these ecosystems” (Pollet et al. 2018:10). Flavobacteriia and other members of the Bacteroidetes phylum were expected to be prevalent biofilm constituents based on prior submerged aluminum studies. For the current study, the order Flavobacteriales dominated the Flavobacteriia assemblage, regardless of site.

Though Cyanobacteria are often classified as free-floating picoplankton, they are also common contributors to biofouling communities as secondary colonizers (Antunes et al. 2019, 2020; Ding et al. 2019; Nayar et al. 2005; Zhang et al. 2019). Cyanobacteria secrete adhesive and mucilage substances, which serve as primary agents of consolidation and integration for the biofouling structure (Del Mondo et al. 2018; Molino and Wetherbee 2008; Nishanth et al. 2021; Rossi and Philippis 2015). Through the photosynthetic process, Cyanobacteria, along with other microalgae and autotrophic eukaryotes within marine biofilms, play a crucial role in energy production and carbon cycling (Ataeian et al. 2022; Behrendt et al. 2012; Goericke et al. 1994; Leao et al. 2012; Stal 2007). In coastal, euphotic waters, Qian et al. (2022:675) noted that “Cyanobacteria are the dominant biofilm component in the western Pacific… but are the minority in biofilms from the western Atlantic, where Verrucomicrobia dominate.” In Hawai‘i specifically, a study of the planktonic and benthic cyanobacteria suggested that the islands’ productive nearshore environments may favor particular Cyanobacteria assemblages that are less abundant in oligotrophic marine systems (Chamberlain et al. 2014). For the current study, Cyanobacteria yielded the most OTUs present in wreck biofilms and absent from the environment, potentially evidence of this bacterial class’s niche specialization within SAWS biofilms.

Contrary to the free-floating Alphaproteobacteria and Flavobacteriia, the inclusion of Planctomycetacia in the SAWS biofilms is clear evidence of sediment also serving as an inoculum for wreck surface communities. This bacterial class's relative abundance in seawater samples was limited to less than 1% at each SAWS, while it ranged between 12.6% - 36.9% across the four sites. Though Planctomycetacia have been documented as submerged aluminum biofilm constituents in the past, the relatively high level of representation is likely indicative of the local Hawaiian environmental influence on community composition. Planctomycetacia are frequently observed in Hawaiian marine sediments, including studies that examined the sedimentary assemblages associated with Kaneohe Bay on the east coast of O'ahu (Brandon 2006; Rusch et al. 2009; Sørensen et al. 2007). There, Planctomycetacia were the most abundant bacterial group, followed by Beta- and Gammaproteobacteria. Within marine sediments, the versatile taxa of the Planctomycetacia class are believed to be heavily involved in the nitrogen cycle and breakdown of detritus, though less is known about the role in biofilms (Vitorino and Lage 2022). Planctomycetacia are a widely-distributed group of understudied "maverick" bacteria, which fall within the Planctomycetes, Verrucomicrobia, Chlamydiae (PVC) superphylum (Wiegand et al. 2018).

Regardless of site or island, the Planctomycetacia assemblage of both biofilm and sediment samples is dominated by the aerobic order Pirellulales, a central taxon for older biofilms and a contributor to both carbon and nitrogen cycling (Fraser 2004; Karačić et al. 2022; Naik et al. 2022). The dominance of this order in both sample types further attests to the plausibility of the sediment microbiome contributing to the species-sorting formation of the SAWS biofilm communities. Planctomycetales, phylogenetically close to Pirellulales, also constituted a major component of biofilms from both Maui and O'ahu, although its contribution to the sedimentary microbiomes is notably less, especially for Maui. The increased representation of Planctomycetales may hint to the potential preference or advantage this bacterial order has for biofilm living.

The ability of the largely sedimentary Planctomycetacia to colonize the surfaces of the SAWSs is likely owed to this bacterial class's adaptation for surface attachment through holdfast structures (e.g. stalks) (Fuchsman et al. 2012; Pizzetti 2010; Storesund et al. 2018). While Planctomycetacia are considered a minor group during the initial stages of substrate colonization, they are routinely observed within mature marine biofilms (Karačić et al. 2022; Odobel et al. 2021; Salta et al. 2013). For the SAWS biofilms, this bacterial class, akin to Alphaproteobacteria, likely forms niche relationships with algae and other autotrophs that are present (Lage and Bondoso 2014). Planctomycetacia are metabolically flexible (aerobic, mesophilic, and neutrophilic), which enables them to thrive in complex environments and respond quickly to environmental changes (Vitorino and Lage 2022). Despite success in isolating members of the Planctomycetacia, the class remains underrepresented in culture studies and its importance in coastal waters is likely underestimated (Pizzetti et al. 2011; Vitorino and Lage 2022; Wiegand et al. 2018; Winkelmann and Harder 2009). Many studies, including the current one, report abundance metrics for Planctomycetacia, but abundance alone is not a measure for environmental importance. For that, a deeper understanding of Planctomycetacia physiology is required to better discern their ecological role.

Similarly, the incorporation of Gammaproteobacteria, which ranked as the third most abundant bacterial class in the SAWS biofilms, can likely be traced to inoculation via the underlying sediment. Numerous studies attest to the abundance of Gammaproteobacteria within marine biofilms, where they are a "major and genuine pioneer" (Pollett et al. 2018:9), benefited by adaptations, such as the ability to degrade polysaccharides and respond to chemical clues from various substrates (Antunes et al. 2020; Edwards et al. 2010; Lee et al. 2003, 2016; Wang et al. 2022). Yet, Gammaproteobacteria are most often associated with marine sediments (Dyksma et al. 2016; Ettoumi et al. 2010; Franco et al. 2017). Within the seafloor, Gammaproteobacteria possess a wide array of ecological roles, including sulfur oxidation, acetate assimilation, hydrocarbon degradation, and dark carbon fixation (Boschker et al. 2014; Catania et al. 2018; Dyksma et al. 2018; Lenk et al. 2011). Locally, in a study of 23 coastal locations around Oʻahu, Gammaproteobacteria were noted as the dominant taxon (Cui et al. 2013). Beachwater corresponding to each of the sediment sampling sites also demonstrated an enrichment in Gammaproteobacteria, with Alphaproteobacteria and Cyanobacteria representing the next most abundant taxa. Sediments from all four SAWS study sites paralleled this Gammaproteobacteria dominance, with the bacterial class ranking first in abundance for Maui and second (behind Planctomycetacia) for Oʻahu.

The relatively muted impact of substrate, in comparison to the environmental influence currently being discussed, is further substantiated by similarities shared between the SAWS biofilms and others formed in Hawaiian waters, albeit on non-aluminum substrates. The composition of inshore and offshore biofilm communities developed on glass, rather than aluminum, collection plates were assessed at several locations on or near Oʻahu's southern coast, including Pearl Harbor and Kewalo Basin (Lema et al. 2019). Taxonomic analysis (16S rRNA amplicon) revealed that all biofilm samples were primarily composed of Alphaproteobacteria, similar to the observations for the SAWS biofilm. Other important bacterial classes included Gammaproteobacteria, Flavobacteriia, and Sphingobacteria. A similar biofilm development study off Ford Island in Pearl Harbor, also using a glass substrate, found that the microbial communities were most abundant in terms of Bacteroidetes (22−26%), likely represented by Flavobacteriia, as well as Alphaproteobacteria (25−28%) and Gammaproteobacteria (17−28%) (Vijayan and Hadfield 2020).

For the former study (Lema et al. 2019), differences were noted between the offshore and inshore sites, primarily as it related to the latter's enrichment of Alphaproteobacteria, specifically the *Rhodobacteraceae* family. Another commonality shared by the inshore and SAWS biofilms, was the relative increase in Cyanobacteria and Planctomycetes as compared to offshore samples. The contribution of both classes to the inshore biofilm communities observed by Lema et al. (2019), however, was less than what was recorded for the SAWS biofilms. Taxonomically, the inshore samples were also more easily differentiated from seawater samples than offshore biofilms were, mainly due to the dominance of specific Cyanobacteria (*Synechococcus* spp.) and Alphaproteobacteria (SAR116 and SAR11 clades) in the seawater and offshore samples. Lema et al. (2019) attributed the overall lower diversity of the offshore biofilm samples to differences in nutrient availability, as the offshore environment was "not exposed to the complex and varied factors that affect coastal waters such as urbanization, river effluents, structures and biota all of which likely contribute to the diversification of coastal biofilms."

This finding was similar to that of Chamberlain et al. (2014) regarding Cyanobacteria and the nearshore environment previously highlighted. Given the proximity of the current study sites to the shoreline, it is likely that the biofilm communities are reflective of the more nutrient-rich conditions of the coast. Taxonomic comparisons with the biofilms from one of the many deep water Hawai‘i aircraft wrecks (NOAA 2017) would enable a more critical evaluation of this assumption. Additionally, as it relates to Cyanobacteria and Planctomycetes, young coastal marine biofilms tend to be dominated by Alphaproteobacteria, Gammaproteobacteria and

Bacteroidetes (comprised mainly of Flavobacteriia, Sphingobacteria and Cytophagia), as demonstrated in both Hawaiʻi (Lema et al. 2019; Remple et al. 2021; Vijayan and Hadfield 2020) and beyond (Antunes et al. 2020; Dang and Lovell 2000; Edwards et al. 2010; Elifantz et al. 2013; Jones et al. 2007; Pollet et al. 2018; Rampadarath et al. 2017; Sushmitha et al. 2021). Thus, the increased presence of Cyanobacteria and Planctomycetes, both secondary colonizers, on the SAWS surfaces is potentially an indicator that these biofilms represent a more mature and stable state of development (Abed et al. 2019; Antunes et al. 2020; Karačić et al. 2022; Muthukrishnan et al. 2014; Pinto et al. 2019; Romeu et al. 2019; Salta et al. 2013; Zhang et al. 2019).

An analog for how the local marine environment influences microbial communities in Hawaiʻi can be seen in the study of coral microbiomes. Based on an analysis of coral samples from Māʻalaea Bay, site of the Hellcat and Helldiver wrecks, Alphaproteobacteria, Actinobacteria, Firmicutes, Spirochaetes, and other Proteobacteria lineages were among the most abundant in the coral tissue communities (Ainsworth et al. 2015). The overall composition of the coral communities, besides the dominance of Alphaproteobacteria, was markedly different than that of the nearby archaeological aircraft sites. On its own, the Maui coral data appears to support the role of substrate shaping bacterial communities. A comparative study of corals from six coastal sites around Oʻahu, however, provides evidence for the impact of the local environment (Price et al. 2021b). The authors found that the microbial community composition differed greatly among all four coral species and among some sites within species. Overall, OTUs affiliated with Gammaproteobacteria (orders Oceanospirillales and Alteromonadales) and Alphaproteobacteria (orders Rhodobacterales and Rhizobiales) were the most abundant among all corals, followed by various bacteria belonging to the Actinobacteria, Bacilli, and

Flavobacteriia classes. The relative abundance of these taxa varied among coral species, which was attributed to the species-sorting effect of the local environment. The latter encompassed a range of factors, again including proximity to coastal contamination sources (e.g. community beaches and terrestrial runoff), as well as environmental parameters (e.g. seawater chlorophyll a level or wave height) and stochastic processes. The surrounding environment's ability to offset the impact that these natural coral substrates have on the microbial community composition, is likely also applicable to the microbiomes associated with artificial substrates, such as aluminum. Interestingly, the proximity of the SAWSs to coral, both in Māʻalaea Bay and off Oʻahu, suggests that the coral microbiomes may also serve as a bacterial reservoir from which wreck biofilm constituents are selected (McDougald et al. 2012; Mugge et al. 2023a; Sweat et al. 2017; Wahl et al. 2012).

Biogeography

Despite being made of similar materials and situated within the same broad Hawaiian marine context, the biofilms of the four wrecks displayed taxonomic differences and similarities that accorded with a wreck site's geographical location. This finding was expected, as the third hypothesis posited that biogeographic patterns would be evident for the SAWS biofilm communities, specifically as it related to similarities between the two sites from Oʻahu and the two sites from Maui. The SIMPER data indicated that Planctomycetacia served as the main taxonomic differentiator between Oʻahu and Maui biofilms, with Alphaproteobacteria, Cyanobacteria, Gammaproteobacteria, and Flavobacteriia constituting smaller sources of variation. For biofilms samples from the two Oʻahu sites, the representation of Planctomycetacia was relatively similar (Corsair: 27.9%; Thunderbolt: 24.9), whereas a large discrepancy existed between the abundance of this class for the Hellcat (25.0%) and Helldiver (17.1%).

This overall difference in Planctomycetacia, however, obscures the potentially more consequential inter-site similarities that exist for SAWSs associated with different islands. Specifically, biofilm samples from the Hellcat site at Maui and the Corsair site at Oʻahu yielded a taxonomic composition that exhibited a relatively higher representation of sedimentary microbes. This unexpected finding is likely attributed to the intermittent burial of these two sites. Sampling at the Hellcat site focused on the aircraft's fuselage and the attached wings, while at the highly-fragmented Corsair site biofilm samples were collected exclusively from a section of the port wing (only remaining aluminum surface). Though both sites were exposed at the time of fieldwork, the planate shape of these wing structures offers little vertical relief, which leads to their occasional interment. Conversely, the nearly-complete Helldiver site sits proud of the seafloor, while the Thunderbolt site remains perched above the sediment as it straddles a narrow channel in the reef flat. Thus, the latter two sites are less exposed to the sedimentary microbiomes, resulting in the inoculation of these microbes appearing less pronounced than it is for the Corsair and Hellcat.

The taxonomic data can be used to demonstrate how the interplay between sediment and site shapes the composition of the wreck biofilms. Planctomycetacia, whose affiliation with the marine sediments has been demonstrated, was in higher abundance than Alphaproteobacteria for biofilm from the Corsair site, while being virtually even for biofilm from the Hellcat site. The Helldiver and Thunderbolt biofilms each exhibited the opposite, with the relative abundance of Alphaproteobacteria, a taxon widely associated with free-floating communities, exceeding that of Planctomycetacia. The environmental microbiome samples observed in the current study further substantiated the interpretation of Alphaproteobacteria linked to seawater and Planctomycetacia serving as an important member of marine sediment communities. Therefore, an increased abundance of Planctomycetacia at the expense of Alphaproteobacteria for the Hellcat and Corsair biofilms supports the notion of a sedimentary influence.

Beyond this discrepancy, the Hellcat and Corsair sites are enriched in terms of other taxa associated with marine sediments. Unclassified Bacteria ranked as the second and third most abundant taxa for Oʻahu (14.8%) and Maui (18.0%) sediments, respectively. Despite being widely studied, the sheer diversity of sedimentary microbes has inevitably left gaps in the taxonomic database (Bech et al. 2020; Hoshino et al. 2020; Vitorino and Bessa 2018). The higher relative abundance of Unclassified Bacteria within the Hellcat (6.3%) and Corsair (9.4%) biofilm samples, as opposed to those of the Helldiver (5.3%) and Thunderbolt (4.4%), is possibly reflective of the sediment's impact.

The heightened presence of Gammaproteobacteria within the Hellcat and Corsair biofilms is less speculative, as this bacteria class constituted the third most abundant taxa for the Hellcat and Corsair biofilm samples (11% each). Conversely, Gammaproteobacteria ranked fourth and fifth for the Thunderbolt (8.7%) and Helldiver (9.3%). The assumption that Gammaproteobacteria represent the sediment's influence on shaping the assembly of SAWS biofilm communities is supported by the fact that for both biofilm and sediment samples of the current study, Chromatiales ranked as the most abundant taxa within this lineage (excluding unclassified Gammaproteobacteria). Chromatiales is primarily made up of phototrophic sulfur oxidizers and has been noted as a prevalent form of Gammaproteobacteria in Hawaiian marine sediments, including those from the east coast of Oʻahu (Cui et al. 2013; Sørensen et al. 2007). Furthermore, *Woeseiaceae*, which are "ubiquitous and consistently rank among the most abundant 16S rRNA gene sequences in diverse marine sediments" (Mußmann et al. 2017:1276), constituted the dominant Chromatiales family in both sediment and biofilm assemblages, thus, attesting to a sedimentary origin.

Other taxa indicative of the sediment influence on the Hellcat and Corsair biofilms, include Deltaproteobacteria and Acidobacteria. While both are minor constituents of the biofilm bacterial assemblages, it is unlikely that their increased abundance at the Hellcat and Corsair sites is coincidental. Deltaproteobacteria have been identified as both "a representative bacterial lineage in benthic environments" (Du et al. 2011:324), and a predominant group in Hawaiian marine sediments (Cui et al. 2013; Gao et al. 2011; Rusch et al. 2009; Sørensen et al. 2007). The relative abundance of Deltaproteobacteria within the Maui sediments (10.6%) was over double that for Oʻahu sediments (4.9%). Yet, the Corsair site in Oʻahu produced the highest Deltaproteobacteria relative abundance (2.7%), followed by the Hellcat site (2.2%), which outranked both the Helldiver (1.0%) and Thunderbolt (1.4%).

The order Desulfobacterales, an SRB, was found to be the dominant Deltaproteobacteria in the aluminum biofilm samples, regardless of island, and sediment samples from Maui. The order Myxococcales, which consists of aerobic or facultatively anaerobic chemoorganotrophs, ranked first for Oʻahu sediment samples. This aligns with previous observations regarding Oʻahu sediments (Sørensen et al. 2007), where Myxococcales tended to dominate the sediment-seawater interface. Yet, Myxococcales abundance was again higher for the Maui Hellcat (0.45%) than the Oʻahu Thunderbolt (0.33%), with the Oʻahu Corsair (0.60%) predicably yielding the highest abundance and the Maui Helldiver (0.28%) the lowest.

Like Deltaproteobacteria, Acidobacteria are also commonly encountered within marine sediments from both around the world (Hoshino et al. 2020; Li et al. 2009; Wang et al. 2012), and more specifically, Hawaiʻi (Cui et al. 2013; Gaidos et al. 2010; Gao et al. 2011; Sørensen et al. 2007). It is believed that this class plays a significant role in the sulfur cycle through the dissimilation of sulfur compounds (Kielak et al. 2016). The Corsair biofilm yielded the highest relative abundance of Acidobacteria (2.0%), followed by the Hellcat (1.6%), despite an enrichment of this taxa within Maui sediments (8.1%) as compared to O‘ahu sediments (5.8%). Neither the Helldiver nor Thunderbolt biofilms produced an Acidobacteria relative abundance greater than 1%. Overall, the biofilm samples from the Hellcat and Corsair sites also yielded higher diversity and evenness statistics, as compared to those of the Helldiver and Thunderbolt. Given the documented sediment influence, this result is not surprising as marine sediments are often diverse and resistant to dominance by a limited number of taxa (Baker et al. 2021; Hoshino et al. 2020; Petro et al. 2017; Underwood et al. 2022).

For the Helldiver (27.4%) and Thunderbolt (21.1%) wreck microbiomes, Flavobacteriia and Cyanobacteria, rather than the sedimentary microbes already discussed, were the next most abundant, following Alphaproteobacteria and Planctomycetacia. Both totals far surpass those yielded by the Hellcat (12.0%) and Corsair (11.1%) biofilm samples. For the latter site, Cyanobacteria relative abundance was only 5.0%, despite the Cyanobacteria-rich waters of O‘ahu previously described. Conversely, Cyanobacteria served as the third most abundant taxa for biofilm from the Thunderbolt site, also associated with O‘ahu. While this may not appear surprising due to the inferred impact the free-floating bacterial communities have on the Thunderbolt’s biofilm, Cyanobacteria also constituted the third best represented taxa among biofilm samples from the Helldiver site, in spite of the aforementioned dominance of Flavobacteriia in the Maui seawater. The abundance of Cyanobacteria, as opposed to Flavobacteriia, for biofilms from both the Thunderbolt, and especially, the Helldiver sites may be indicative of Cyanobacteria’s ability to either outcompete or succeed the pioneering

Flavobacteriia within biofilm settings. In any case, the co-occurrence of these two classes and Alphaproteobacteria as three of the four most dominant taxa for the Helldiver and Thunderbolt sites suggest that free-living, planktonic communities, rather than those associated with sediments, served as primary inoculum for these sites.

Implications for MIC

This study's final research objective was focused on gleaning insights into how the microbial data may provide information on the potential of MIC affecting the SAWSs in Hawai'i. This was, of course, performed through a comparison of biofilm communities associated with corroded and non-corroded surfaces. Yet, unlike Price et al. (2021a) and Mugge et al. (2019a), this study was unable to identify distinct associations between corrosion and microbial community composition. While corroded wreck surfaces were sampled, it is currently unclear to what extent the corrosion can be confidently attributed to microbial activity. Conclusive evidence of MIC is generally difficult to discern, as highlighted by Little and Lee (2022:182), who stated that "[t]here are no morphological indicators for MIC." Thus, the physical impacts that can be attributed to MIC (e.g. pitting) are not necessarily unique to this corrosive pathway. This is because MIC itself is not a form of corrosion, but rather a process in which microbial activity changes microenvironmental conditions resulting in the activation of a corrosion mechanism. Examples relevant to the current study include unevenly deposited biofilm, where locations under the respiring microbial colonies can become oxygen depleted through the buildup of consolidative biofilm substances and bacterial metabolism (Little and Lee 2007; Procópio 2019). The significant presence of biofilm-forming microbes, such as Cyanobacteria and *Rhodobacteraceae*, and other aerobic bacteria suggest this is possible for the Hawai'i SAWSs. Furthermore, the co-occurrence of strictly and facultatively anaerobic microbes, including various Deltaproteobacteria, Clostridiales, and Cytophagales, lends credence to the idea of oxygen depletion within the biofilm layer. Thus, these conditions imply the potential existence of an oxygen concentration cell, where the oxygen-exposed areas adjacent to the biofilm become cathodic, resulting in the transfer of electrons from the anodic metal under the biofilm and increased metal loss (e.g. pitting) (Hamilton 2003; Van Loosdrecht et al. 2002).

The contribution of SRB to the biofilm communities represents another way in which MIC may be occurring at the four SAWSs. Though a minor constituent, *Desulfobulbaceae*, an anaerobic SRB, displayed a specific affiliation with the wreck biofilms. Like most SRB, *Desulfobulbaceae* reduce naturally-occurring sulfate into sulfide and the resulting metabolite can increase corrosion through reactions with the underlying metal substrate (Guan et al. 2017; Kuever 2014; Marty et al. 2014; Phan et al. 2020). The sediment influence noted earlier for the Hellcat and Corsair biofilms may have site preservation implications, as Liu et al. (2014:375) found that the corrosion rates of aluminum anodes placed in marine sediments "were enhanced substantially by SRB." A similar conclusion was reached by Beech and Campbell (2008), who were able to correlate the increased corrosion of partially-submerged steel structures with the presence of specific microbes found in both the biofilm and surrounding sediment, including SRB and sulfur-oxidizing bacteria. The latter can use SRB metabolic sulfides during their own metabolism, resulting in the production of sulfuric acid, which can also be highly corrosive (Cragnolino and Tuovinen 1984; Iverson 1987). For each wreck, the sulfur-oxidizing Chromatiales, which relies on sulfide as its reducing agent during photosynthesis (Imhoff 2005), represented a significant component of the biofilm community. Within the SAWS biofilm, the existence of Chromatiales and anaerobic *Desulfobulbaceae* is likely supported through the aforementioned oxygen gradients created by secretion buildup and the aerobic constituents' metabolic activities. The latter also provides the requisite carbon source (e.g. organic waste) for numerous forms of anaerobic metabolism (Caruso 2020; Dang and Lovell 2016; Salta et al. 2013). Thus, two of the requisite conditions for MIC (differential oxygen zones and corrosive metabolite producing bacteria) are present within the biofilms of the SAWSs. Understanding the extent to which MIC is actually occurring at these sites, however, will require additional lines of evidence that are discussed next.

Future Directions

The taxonomic data presented provides both a font of information regarding the bacterial communities that colonize SAWSs in Hawaiʻi and a hypothetical case for the existence of MIC. As with any research, however, there are always ways of supplementing and improving the methodologies used here. For the current study, geographical distance between the sample sites and laboratory facilities was a primary factor in encouraging the taxonomic focus of this initial research, as opposed to more sophisticated forms of molecular analyses described below. This project also represented the first attempt at the in situ collection of SAWS biofilm, thus there were uncertainties regarding the sampling method's ability to obtain sufficient genetic material. Now equipped with an understanding of the bacterial communities present and confirmation of the collection method's success, follow up studies can employ more specialized analyses targeting gene functionality and other facets of a site's microbiome.

Concluding this article with a 'Future Directions' section is intended to ignite conversations about how the current research can be built upon to further elucidate information on the microbiology of SAWSs. The future directions can be essentially divided into three categories, with the first focused on increasing the overall dataset by obtaining more samples. These efforts can include adding more SAWSs, both within Hawaiʻi and beyond, which should enable a more thorough examination of the various factors influencing biofilm composition. Additionally, the impact of seasonality could be assessed (Anderson 1995; Antunes et al. 2020; Bellou et al. 2020; Chiu et al. 2005; Misic and Covazzi Harriague 2019; Oberbeckmann et al. 2014; Passarelli,et al. 2015; Price 2020), though in Hawai‘i seasonal fluctuations in water conditions are often minor in comparison to locations with less stable climates. The effect of substrate may also be further investigated by targeting specific components of an aircraft that were known to be made of different aluminum alloys and other metals (Ouissi 2020; Ouissi et al. 2019; Rocca et al. 2021). For the current project, sample areas were chosen based on the presence of visibly corroded and uncorroded aluminum surfaces. Given the metallurgically-complex makeup of aircraft, future sampling efforts should be more discerning and target wreck surfaces that yield information on the communities associated with various alloys, treatments (e.g. paint), and chemical residues (Brunet et al. 2024; Montané et al. 2023).

The second category of future directions is largely methodological and intended to supplement the current amplicon sequencing data. While phylogenetic surveys that target variation pertaining to a singular gene (e.g. 16S rRNA) provide detailed descriptions of community composition, as presented here, they do not necessarily offer direct evidence of a community's functional capabilities (Burke et al. 2011; Ding et al. 2019, 2021; Knisz et al. 2023; Lopez 2019; Mugge et al. 2021; Sanli et al. 2015; Zhang et al. 2019). The construction of functional gene profiles through metagenomics has been used as a way of linking phylogeny and function in the investigation of marine biofilm communities (Hemdan et al. 2019; Imchen et al. 2022; Leary et al. 2014; Schmeisser et al. 2017). Within the field of MIC research, examining functional gene families through metagenomic approaches (e.g. shotgun sequencing) has proven valuable in discerning correlations between gene abundances and areas of increased metal loss (Avelino-Jiménez et al. 2023; Kotu et al. 2019, 2024; Mugge 2018; Procópio 2023).

Additionally, cell activity, as measured by ATP and RNA sequencing (metatranscriptomics), has been used as a supplement to traditional community and metagenomic analyses in studies of MIC (Gomes et al. 2023; Krohn et al. 2021). For example, Salgar-Chaparro et al. (2020) attributed the corrosion of steel coupons with increased quantities of active cells, as opposed to cell abundancies and taxonomic composition. Detection and monitoring tests that rely on the identification of proteins as biomarkers (metaproteomics) correlated with corrosion have also been explored (Chatterjee et al. 2021; Dupree et al. 2020; Pilloni et al. 2022), while the quantification of corrosive metabolites (metabolomics) represents another method of assessing MIC prevalence (Beale et al. 2014; Bonifay et al. 2017; Mand et al. 2016; Marks et al. 2021). The combination of the current taxonomic data with future results yielded from metagenomic sequencing, cell activity analysis, protein biomarkers, and metabolite quantification offers the potential for detailed insights to the relevance of MIC to SAWSs. The feasibility of utilizing these methods will, of course, be challenged by restrictions related to cost, specialized equipment, and qualified personnel inherent to these methodologies (Knisz et al. 2023). Furthermore, specificities pertaining to minimum sample size, degradation risk, and handling may be incompatible with certain datasets (Han et al. 2015; Imdahl and Saliba 2020; Lu et al. 2022; Ozsolak and Milos 2011; Van Vliet 2010).

Finally, incorporating interdisciplinary lines of evidence, such as corrosion and photogrammetric data, is essential for accurate MIC assessments. Little and Lee (2022:182) listed three requirements for an MIC diagnosis, with the first being “a sample of the corrosion product or affected surface that has not been altered by collection or storage.” For archaeological sites, such as SAWSs, removing corroded elements may be neither feasible, nor legal. There are, however, minimally-intrusive alternatives, including the photogrammetric documentation of a site, which can be used to identify various forms of corrosion. Three-dimensional models created from the photogrammetric data can be chronologically compared using point cloud deviational analysis to discern areas of change and metal loss (Cvetkovic 2020; Holst et al. 2017; Neuner et al. 2016; Rossi et al. 2019; Yamafune 2024). The optical evidence for corrosion can be combined with electrochemical measurements (E_{corr} and pH) that can indicate whether a metal surface is in a state of active corrosion (MacLeod 2002; Richards and Carpenter 2015), though such tests are incapable of distinguishing MIC from abiotic corrosion.

Thus, the second requirement is the "identification of a corrosion mechanism, consistent with the properties of the material and identification of microorganisms capable of producing the corrosion mechanism" (Little and Lee 2022:182). Achieving this benchmark necessitates the use of controlled environments in order to establish relationships between the substrate of interest (e.g. aluminum alloys used in WWII aircraft) and microbes identified from the biofilm communities. Laboratory experiments that assess metallurgic properties and reactions to the presence and activity of specific taxa can help elucidate the corrosion mechanism (Dai et al. 2016; Lu et al. 2023b; Mugge et al. 2019b; Salerno et al. 2018; Vejar et al. 2022). Finally, the third criterion for an MIC diagnosis is the "demonstration of an association of the microorganisms with the observed corrosion" (Little and Lee 2022:182). Spatially-informed taxonomic data, as was presented here, paired with laboratory observations and additional microbial bioinformatics can be used to recognize those associations.

Conclusion

This study provided the first taxonomic assessment of the biofilm microbiomes associated with four SAWSs off the coast of Hawai‘i. Overall, biofilm samples from the aluminum wreck surfaces were distinct from sediment, seawater, and biofilm from non-aluminum components. The microbial communities reflected a mixture of bacterial types that are common to submerged aluminum and the Hawaiian marine environment, including the sediment and seawater. Inter-site comparisons revealed an unexpected similarity of the biofilm microbial communities between two sites, indicative of a pronounced sediment influence on the biofilm's taxonomic composition. The biofilm data provided circumstantial evidence of MIC, as inferred through the assumed deoxygenation of metal under the biofilm and the presence of specific taxa involved in the sulfur cycle. When compared to non-corroded areas, there were, however, no conclusive associations between certain bacterial taxa and the corroded wreck surfaces.

The data can now serve as a both a confirmation of the biofilm collection methodology and a starting point for follow-up studies. The results can be utilized as a taxonomic baseline for tracking changes to the bacterial community in parallel with a site's deterioration. Furthermore, the microbial communities provide a point of comparison for investigations into the effect increased ocean warming and acidification has on submerged heritage resources. In discussions regarding the nexus of archaeological management and climate change, shifting microbiomes is often touted as a potential consequence with negative effects for underwater sites (Daly 2017; Gregory et al. 2022; May et al. 2008; Paxton et al. 2023; Pearson et al. 2010; Wright 2016). Yet, without the necessary baseline data, evaluations of this assertion are impossible.

Future sampling efforts should also seek to advance the preliminary research presented here by employing metagenomic and other molecular techniques to elucidate information on functional gene profiles, cell activity, corrosion biomarkers, and metabolite quantification. To truly make a MIC diagnosis, however, other lines of evidence are required, including electrochemical measurements, laboratory experiments, and photogrammetric documentation. More definitive statements regarding the realistic importance of MIC to SAWSs will only be achieved through an interdisciplinary approach, for which the microbial composition of biofilm is one piece of a much larger puzzle.

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Chapter 5: Conclusion

Implications of the Current Study

The employment of microbiological research to questions fundamentally concerned with heritage preservation underscores the utility of interdisciplinary approaches. Yet, for the value of this dissertation to be fully realized, the knowledge ascertained should have practical applications to the management of submerged aircraft wreck sites (SAWSs), especially those in Hawaiʻi. To illustrate this point, the following discussion will outline what the study accomplished, how the current data can be used, and future directions for this line of research. Though this dissertation could not formulate conclusive statements regarding the impact of microbiologically-influenced corrosion (MIC) on SAWSs, there is still scientific value in being the first to investigate this phenomenon. The results inform future studies on what methodological approaches have been taken, thus highlighting aspects of this study that both worked and did not work. From there, speculation can begin on additional lines of evidence that are needed, while using the initial taxonomic data presented here as a baseline. Ultimately, it should be apparent that the findings serve as both an insight into the nexus of archaeological management and marine ecology, as well as a starting point for more sophisticated forms of analyses.

Biofilm Collection Method

The first success of this study was the establishment of an effective biofilm sampling protocol, as highlighted in Chapter 3, and further supported by the data presented in Chapter 4. Chapter 3 discusses how previous MIC studies relied on either destructive forms of sampling that required the removal of concretions, corrosion products, and wreckage debris, or proxies for wreck substrates, such as test coupons and underlying sedimentary communities. Thus, the methodology presented here represents a minimally-invasive, in situ alternative. Of course, there are practical limits to using this method of collection, primarily as it relates to depth. The sites sampled in this study were between 4-20 m deep, allowing for single tank air dives. Each collection dive took between 45-60 minutes, resulting in 5-6 biofilm samples per dive. The syringe method should be amenable to use by technical divers capable of reaching deeper depths, though for sites beyond the safe operating depths for divers, it could be more difficult. Fleming et al. (2013), however, described the collection of microbial mat samples using syringes and a remotely operated vehicle (ROV). According to the authors, “The manipulator arm gripped the syringe and moved it until the tip was just touching the surface of a mat; finally, the plunger was retracted by pulling the lanyard with the other manipulator arm resulting in collection of surficial mat layers” (Fleming et al. 2013:117). Whether ROV attachments have the dexterity to collect attached biofilm, as opposed to the less adhesive mat materials, bears consideration. If this operational hurdle can be cleared, deepwater wrecks, such as those in the Gulf of Mexico described by Church et al. (2007), and other forms of underwater cultural heritage (UCH), could be sampled for biofilm, given the requisite ROV.

The methodology used is neither technically, nor technologically, complex, thus making it easily reproducible. Replicate studies are benefited by the affordability and speed of the protocols puts forth. The plastic syringes and falcon tubes used can be purchased in packs of 40-50 for less than $100 USD. Other supplies, including the polypropylene spatulas, serological pipettes, and syringe filter (for water sampling, can also be purchased at reasonable prices. The lack of specialized equipment, outside of the YSI meter, makes biofilm collection more feasible for management agencies. In Chapter 3, the possibility of follow up collection efforts falling under the domain of ‘citizen science’ was also emphasized (Silvertown 2009), with the non-profit Naval Exploration and Research Divers (NERD) highlighted as a potential partner in Hawaiʻi. Admittedly, the expenses associated with the laboratory analysis, both in terms of consumables (e.g. DNA extraction kits) and equipment, likely negates the ability of management agencies and citizen scientists to perform this portion of the project. In such cases, partnerships with academic institutions who have access to the requisite facilities offers a viable way forward.

Yet, the implications of the sampling method's viability for SAWSs extends beyond repeating the current study in hopes of providing longitudinal and geographical comparisons. Marine biofilms have increasingly become a major point of focus for understanding ecological structure, with specific attention paid to the roles of marine biofilm in carbon sequestration and dictating larval settlement of macrofouling organisms (Ataeian et al. 2022; Cooney et al. 2023; Dang and Lovell 2016; Hadfield 2011; Hadfield et al. 2014; Jiao et al. 2014; Qian et al. 2022; Rajitha 2020). Perhaps most germane to SAWSs was the success of isolating extracellular, or environmental, DNA (eDNA) from marine biofilms. The incorporation and stabilization of eDNA in biofilm, through binding with certain compounds, enabled several environmental monitoring studies focused on key (e.g. protected, commercially-valuable, invasive) marine species (Rivera et al. 2022; Tuck et al. 2022; Wood et al. 2020). In 2023, this approach was applied off the coast of Saipan, in an attempt to discern both the artificial reef role that SAWSs play and how these sites support marine life populations (NOAA 2023). The collection method was chosen, in part, because of the proven success of obtaining biofilm from SAWSs during the 2021 fieldwork associated with this dissertation.

It would be misleading, however, to present the biofilm collection method as a novel innovation. Rather, specific decisions regarding which materials to use and the actual collection process were informed by practical constraints of working underwater and the experiences of others. The research of Pochon et. al (2015) was instrumental in demonstrating the efficacy of various sampling implements (i.e. modified syringe, sponge, underwater tape, and swab) and confirming the viability of syringes in obtaining sufficient microbial material for DNA sequencing. Equally informative were personal communications with two of the study's authors, Drs. Xavier Pochon (Cawthron Institute) and Anastasija Zaiko (Cawthron Institute), as well as the advice from Drs. Loïc N. Michel (University of Liège), Gail Ashton (Smithsonian Institute), and Costantino Vetriani (Rutgers University). Conversations with these individuals led to key considerations, including the need for biofilm dislodging tools, the use of suction for collection, and working in two-person collection teams. Consultation was sought on the basis that each had previously performed marine biofilm sampling projects. While none were focused on UCH resources, the prior studies used the microbiological analysis of biofilms samples to investigate a multitude of issues. These included assessments of climate change's impact on microbial communities, ship fouling in the spread of invasive species, the evolution of bacterial metabolism, and food web structures (Clark et al. 2019; Michel et al. 2019; Patwardhan et al. 2018; von Ammon et al. 2018). Marine biofilm's relevance to a diversity of topics underscores the utility of sound sampling techniques. Thus, the syringe method presented can be applied to a variety of in situ marine biofilms, especially those on artificial surfaces.

Biofilm Data Relevant to Submerged Aircraft Wreck Sites

Conclusions regarding the viability of the biofilm collection methodology are made possible by the actual microbiological data. Prior to fieldwork, biofilm sample contamination from the surrounding environment, namely sediment and ambient seawater, was a chief concern. There was less doubt that microbial material would be collected, so the uncertainty arose from whether the DNA sequencing results would be reflective of genuine SAWS biofilm communities, or simply a composite of sediment and seawater inclusions. Based on the dataset structure, it is apparent that biofilm samples share significant similarities with one another, while remaining distinct from the environmental categories. This was consistently demonstrated by using ANOSIM tests, a non-parametric analysis of similarity by grouping variables, to contrast the different sample types. The statistical strength of these assessments is bolstered by a sufficient sample count, with over 40 biofilm samples across the four wrecks. Taxa common in all aluminum biofilm samples enabled inferences into a core SAWS microbiome. These findings remained consistent for each of the sites, representing the coasts of two separate islands. The validity of the identified biofilm communities is further substantiated by comparisons with the data from previous studies investigating aluminum biofilms, which indicate several bacterial phyla (e.g. Proteobacteria and Bacteroidetes) as common constituents (Bellou et al. 2012; Hoellein et al. 2014; Lee et al. 2014; Price 2020; Zhai et al. 2022; Zhang et al. 2019b). Divergence in the taxonomic composition of the current dissertation's biofilm samples and those associated with previous submerged aluminum contexts could reasonably be attributed to local species sorting. For example, both Planctomycetota and Cyanobacteria represent a considerably large component of the microbial assemblage from the Hawaiʻi SAWSs, although they are either absent or less abundant in the other datasets. The high relative abundance of these two taxa has, however, been observed for other Hawaiian marine biofilms, albeit from non-aluminum substrates (Lema et al. 2019; Vijayan and Hadfield 2020). Finally, the effects that sediment-site interactions have on the biofilm communities was perhaps the most unexpected result. Notable similarities shared by the biofilms from the Maui Hellcat and the Oʻahu Corsair existed, despite documented interisland differences between the environmental microbiomes associated with Maui and Oʻahu.

Potential Evidence of Microbiologically-Influenced Corrosion

As informative as these results may be, their significance remains largely under the domain of microbiology. Yet, the rationale for undertaking this project was not motivated by purely ecological concerns, but rather how the ecology of SAWS microbiota can be used to infer the potential of MIC. Thus, conclusions strictly pertaining to the uniqueness of SAWS biofilm microbiomes and the factors that shape their composition are of little use to archaeologists. For the data to be of service to UCH managers, the research's implications for understanding threats to in situ preservation must be made explicit. This was addressed in the "Microbiologically-Influenced Corrosion" portion of Chapter 4's discussion section, mainly as it relates to two key MIC pathways: oxygen concentration cell and corrosive metabolites. Regarding the former, the uneven allocation of biofilm and deoxygenation of the original surface metal is of concern (Little and Lee 2007, 2022). While the taxonomic data indicates the existence of bacterial biofilms colonizing wreck surfaces, the distribution of these colonies is less clear. For steel shipwreck sites, biofouling is characterized by a layer of marine concretion and thickness can be measured using vernier calipers (Richards and Carpenter 2012). Given that biofilm is often on a microscopic scale, with thicknesses in the micrometers, visual assessments of distribution and measurements of the buildup are impossible.

Confirmation of the requisite hypoxic environment for an oxygen concentration cell is also difficult to obtain. The taxonomic composition of the SAWS biofilms suggests that is possible based on the co-occurrence of aerobic and anaerobic microbes. Oxygen-dependent constituents, such as Alphaproteobacteria and Cyanobacteria, likely provide the necessary consolidatory substances for the wreck biofilm structures (Brito et al. 2022; Dang et al. 2008; Dang and Lovell 2002; Elifantz et al. 2013; Kviatkovski 2015; Rossi and De Philippis 2015). As secretions and microbial metabolism increase, the oxygen levels within the biofilm may decrease, eventually enabling inhabitation by anaerobic bacteria (Dang and Lovell 2016; De Carvalho 2018; Finnegan et al. 2011; Jones et al. 2007; Pollet et al. 2018; Qian et al. 2022). Examples of the latter, including various Deltaproteobacteria, Clostridiales, and Cytophagales, were identified and attest to a hypothetical deoxygenated environment within the biofilms. Yet, the mere existence of hypoxic, or even anoxic, conditions is insufficient in confirming an oxygen concentration cell. The area of low oxygen must be juxtaposed to a well-oxygenated surface, thus enabling the transfer of electrons associated with the corrosion process (Lewandowski and Beyenal 2008; Picioreanu and van Loosdrecht 2002).

The creation of an anaerobic environment is also relevant to the second MIC pathway considered, which involves the production of corrosive metabolites. Much of the emphasis has been on anaerobic sulfate-reducing bacteria (SRB), due to their well-documented role in the biocorrosion of submerged metals, including aluminum (de Andrade et al. 2020; Guan et al. 2017, 2020; Jaume et al. 2022; Javed et al. 2017). For the four SAWSs in Hawaiʻi, differences in SRB abundance amongst sediment samples from Maui and Oʻahu were not evident in the biofilm samples. Though Maui sediments produced a higher SRB abundance, it was the biofilm samples from Oʻahu's Corsair site that yielded the highest SRB abundance, while Maui's Helldiver site yielded the lowest. The other Oʻahu site, the Thunderbolt, compared favorably to the SRB-depleted Helldiver and the Maui Hellcat more reminiscent of the Corsair. The suspected cause of this discrepancy is attributed to intermittent burial of the two less-complete aircraft (Corsair and Hellcat) based on the assumption that the sediment serves as the primary SRB reservoir. Though the SRB abundances yielded by the SAWS biofilm samples were relatively modest, they do not negate the possibility of SRB-induced corrosion. Additionally, the low SRB sequence totals could theoretically be dismissed as accidental inclusions from the underlying sediment. Enrichments of SRB are routinely noted in studies of marine sediments (Kasten and Jørgensen 2000; Orphan et al. 2001; Purdy et al. 2002), with the current data mirroring an overall higher SRB abundance within the sediment samples, as compared to the biofilm ones. A taxonomic comparison between the SRB assemblages associated with the SAWSs and those linked to the sedimentary microbiome, however, revealed an interesting taxonomic affiliation. Had the SRB sample populations within biofilms simply been the result of sedimentary intrusions, it would stand to reason that this should be reflected in the taxonomy. Yet, biofilms, except for several samples from the O‘ahu Thunderbolt site, were consistently characterized by Desulfobulbaceae as the dominant SRB taxon. Conversely, sediment samples yielded SRB assemblages dominated by Desulfobacteraceae. If the biofilm samples are not merely the reflection of sedimentary SRB populations, then what is causing these divergences? Though this question remains unanswered at the present time, future studies may reveal an ecological niche that Desulfobulbaceae fulfills within aluminum marine biofilms. Whether that niche contributes to the corrosion process should be of interest to UCH managers.

It should be noted that the relative rarity of SRB in the SAWS assemblages should not be interpreted as a lack of ecological and community importance. Much of marine microbiology has focused on discerning the roles and functions of the most abundant microbial taxa (Galand et al. 2009; Lynch and Neufeld 2015; Pedrós-Alió 2006, 2012; Sogin et al. 2006), a partiality that this dissertation is occasionally guilty of. The world’s oceans, however, are home to a nearly unquantifiable diversity of bacterial species, the majority of which fall under the ‘long-tail of low-abundant taxa’ (Galand et al. 2009; Huber et al. 2007; Kirchman et al. 2009; Pedrós-Alió 2006). Furthermore, abundance itself can be a dynamic metric, as one study found that over half of the bacterial taxa alternated between being ‘rare’ and ‘abundant’, while only 12% remained permanently rare throughout the study’s duration (Campbell et al. 2011). Thus, consideration of the ‘rare biosphere’, whether that is in planktonic, sedimentary, or biofilm systems, remains a critical aspect of understanding functional potential. This is impart due to the misnomer that abundance and activity are necessarily correlated positively. Multiple investigations have revealed that rare taxa can be amongst the most active metabolically across different aquatic environments (Aanderud et al. 2015; Campbell et al. 2011; Jia et al. 2019; Jones and Lennon 2010). It is believed that rare taxa exploit micro-niche conditions, taking advantage of variations in parameters such as oxygen and pH (Jia et al. 2019, Lynch and Neufeld 2015; Pascoal et al. 2021; Pedrós-Alió 2012; Sogin et al. 2006).

Similar to overall activity, the ecological importance of the rare biosphere may also be disproportionately increased. A number of “gatekeeper function” (Lynch and Neufeld 2015:223) performed by rare microbial taxa have been identified, including nitrification, nitrogen fixation, degradation of particular chemical substrates, and other niche metabolic activities (see Jousset et al. 2017:Table 1 for a full list of functions and relevant studies). Pester et al. (2010) highlight the example of the SRB *Desulfosporosinus*, a taxa that made up less than .01% of a soil assemblage in a German peatland. Yet, the majority of sulfate reduction and carbon assimilation occurring in this sedimentary system was attributed to this bacterium, hinting at this taxon’s status as ‘keystone species’. Thus, the SRB observed for the SAWS biofilms, though low in abundance, may still exert significant influence on community dynamics and nutrient flow. Even when rare taxa that remain dormant, serve as reservoirs of diversity (i.e. seed banks) with taxonomic abundance shifting according to environmental conditions and competition (Aanderud et al. 2015; Caporaso et al. 2012; Gibbons et al. 2013; Lennon and Jones 2010; Pedrós-Alió 2006, 2012). These microbial caches can enable resilient responses to disturbances and prevent extinction.

Baseline Data for Future Studies

Finally, the SAWS biofilm communities described for this dissertation represent a snapshot of a dynamic consortium that is prone to environmentally-induced change (Antunes et al. 2019; Briand et al. 2022; Dobrestov et al. 2018, 2019; Misic and Covazzi Harriague 2019; Salta et al. 2013). Thus, the value of the taxonomic data is not only what it reveals about current wreck microbiomes and the relevance of MIC, but also includes the contribution it can make for understanding processes of change. The impact of climate change, namely through the effects of warming oceans and elevated carbon dioxide partial pressure (pCO2), will likely constitute a major influence on the development, growth, and function of marine biofilms moving forward (Abirami et al. 2021; Arromrak et al. 2022; Baltar et al. 2019; Caruso and Ziervogel 2022; Coelho et al. 2013; Collins et al. 2020; Dang and Chen 2017; Ducklow et al. 2010; Kalbande et al. 2023; Lindh et al. 2013; Hutchins and Fu 2017). Establishing baseline data, as was achieved in the current dissertation, is an essential step in being able to determine the specific effect shifting ocean conditions have on microbial communities. For heritage preservation, the exact nature of how these changes in the marine microbiota will affect sites is a question that has been posed before, though little has been done to discern concrete answers (Daly 2019; Fors and Björdal 2013:37; Pearson et al. 2010; Wright 2016).

Past research can inform site managers on the anticipated taxonomic alterations associated with climate change and other environmental disturbances (i.e. eutrophication), specifying which microbes are most likely to take advantage of the new marine conditions. With respect to the Hawai‘i SAWSs, subsequent sampling efforts, using a similar methodology as this study, can then assess the accuracy of these predictions by longitudinally comparing biofilm compositions. If increased site corrosion at one of the four sites correlated with an observed community change that can be linked to a known climate change impact, then a definitive connection between climate and SAWS management may be provided. The hypothetical value of the initial taxonomic data gathered from the Hawaiian aircraft, however, is not limited to archaeologists and UCH managers. Interdisciplinary implies a bilateral relationship, in which the separate disciplines can mutually benefit from the exchange of information and methods (McDonald et al. 2018). Thus, climate scientists, whose interests may be completely divorced from heritage preservation, can utilize serial SAWS biofilm datasets as additional lines of evidence to draw upon.

Germane to the SAWS biofilms, current research pertaining to the effects of elevated ocean temperatures on marine biofilms, using both mesocosm experiments and in situ sampling, has yielded mixed results (Kent et al. 2018; Khosravi et al. 2019; Mensch et al. 2020; Price and Sowers 2004; Russell et al. 2013; Stratil et al. 2013; Sushmitha et al. 2023; Wahl et al. 2012; Witt et al. 2012). The growth of certain microbes can be stimulated, while others responded negatively. In general, microbial activity and biomass is expected to increase in coastal waters under warmer ocean conditions, as temperatures approach the optimal growth temperature for mesophilic bacteria (~37°C, range: 20 to 45 °C) (Schiraldi and De Rosa 2015). For example, Stratil et al. (2013) observed a 2-fold increase in Rhodobacteraceae, the primary SAWS biofilm constituent, in response to increased water temperatures. Kent et al. (2018) also noted 'high-temperature adaptations' in *Roseobacter*, a genus within Rhodobacteraceae, as responsible for increased biofilm development. If biofilm development is positively correlated with rising temperatures, the increased bacterial colonization could result in a higher likelihood of oxygen concentration cells forming on SAWS surfaces. This relationship, however, is not always as straightforward, as illustrated by Cyanobacteria, another key component of the SAWS biofilms. Warmer ocean waters are expected to correlate with increased exposure to both photosynthetically active radiation and ultraviolet, which favors photosynthetic biofilm constituents, such as Cyanobacteria and microalgae (O'Neil et al. 2012; Paerl and Paul 2012; Wagner and Adrian 2009). Yet, light-independent studies of the effect of elevated temperature suggested an increase in Gammaproteobacteria at the expense of Cyanobacteria (Witt et al. 2012a).

The intricacy of climate change’s effect on marine biofilms is compounded by ocean acidification, the “other CO2 problem” (Doney et al. 2013:169). The elevated pCO2 responsible for acidification can be a favorable stimulus for two of the most relatively abundant taxa in the SAWS biofilm samples: Cyanobacteria and Flavobacteriia (Bach et al. 2017; Fu et al. 2007, 2008; Liu et al. 2010; Lomas et al. 2012; Morán et al. 2010; Ng and Chiu 2020; O'Neil et al. 2012). The former depends on the uptake of dissolved atmospheric CO2 during photosynthesis (Badger and Price 2003), though symbiotic relationships with diatoms within biofilms may be disrupted as increased pCO2 has been associated with lower diatom densities (Peck et al. 2015). Mackey et al. (2015:74) concluded that the overall benefits of increased acidification for photosynthetic marine microbes, such as cyanobacteria, may also be offset “by other negative effects, such as possible respiratory costs from low pH.”

Witt et al. (2012b) noted an enrichment of Flavobacteriia under elevated acidification that came at the expense of Rhodobacteraceae and other members of the Marine Rosebacter Clade (see Buchan et al. 2005 for overview of this bacterial lineage). The decrease in Rhodobacteraceae contradicts the observations of Harvey et al. (2020), who noted an enrichment of Alphaproteobacteria, including Rhodobacteraceae, and several members of Gammaproteobacteria, most notably Chromatiales (the dominant Gammaproteobacteria in the SAWS biofilms) under elevated pCO2 conditions. Interestingly, Harvey et al. (2020) also noted other Gammaproteobacteria, including Alteromonadales, Oceanospirillales and Vibrionales, were all negatively correlated elevated pCO2. The exact mechanisms behind the impact of acidification on marine microbes are as equally varied as the bacterial responses (Das and Mangwani 2015; Harvey et al. 2020; Kerfahi et al. 2023; Patil et al. 2011; Webster et al. 2013; Witt et al. 2011). For biofilm, the most relevant effects are believed to be the weakening of the adhesion substances that provide biofilm its structure and changes to vital chemical signals, such as those that regulate gene expression in response to population density (i.e. quorum sensing) (Decho et al. 2009; Hmelo 2017; Nelson et al. 2020). The complex interplay between increased pCO2 and marine biofilms is highlighted by Dobretsov et al. (2019:590) who summarized that "[r]eports of the impact of ocean acidification on biofouling communities and their bioactive compounds are contradictory, indicating that responses are community dependent." The particularity of this relationship places a premium on site-specific sampling, as microbial responses to climate change are inherently resistant to generalizing statements.

Climate change on a global, long-term scale is not the only anthropogenic impact on the ocean's chemistry that warrants attention. Nutrient enrichment of the world's coastal waters is becoming increasingly common, with terrestrial runoff serving as the primary culprit (Rabalais et al. 2009). Distance from the point source pollution creates water quality gradients, as nutrient, light, and oxygen levels are impacted (Witt et al. 2012a, 2012b). Similar to warming and acidification, the change in certain ocean conditions that accompany nutrient enrichment can significantly alter the bacterial community composition of marine biofilms. Eutrophication has been correlated with a general increase of bacterial diversity and richness in marine environments (Lawes et al. 2016; Melchers and Jeffery 2006; Ng and Chiu 2020; Salgar-Chaparro et al. 2020). In a quantitative model for the long-term corrosion of submerged iron, Melchers (2014) suggested that nutrient increases (e.g. dissolved inorganic nitrogen) resulted in heightened microbial activity across the spectrum, including those processes linked to MIC. Thus, nutrient enrichment has generally been conceptualized as a contributor to the biocorrosion of UCH sites.

The influx of dissolved inorganic nitrogen and other molecules associated with runoff can also trigger shifts in taxonomic dominance, as has been described for the transition from Proteobacteria (e.g. Alpha and Gamma) to Bacteroidetes, namely Flavobacteriia (Remple et al. 2021). Harmful algal blooms (HABs), which significantly deplete dissolved oxygen levels, are another undesirable consequence of excessive nutrients. Increasing in frequency at a worrying level, HABs have been correlated with increases in Flavobacteriia and Cyanobacteria (Gajardo et al. 2023; Griffith and Gobler 2020; Hundell 2008; O'Neil et al. 2012; Paerl et al. 2016; Teeling et al. 2012; Wemheuer et al. 2014; Wurtsbaugh et al. 2019; Zhang et al. 2018). For the Hawai'i SAWSs, the occurrence of these two taxa appears correlated, trailing only Alphaproteobacteria and Planctomycetacia as the most abundant biofilm constituents for sites not subjected to intermittent burial. Increases in the representation of the two more eutrophic bacteria may indicate heightened runoff contamination. Of course, confirmation can be provided by water sampling that assesses parameters such as total dissolved inorganic nitrogen (ammonia, nitrate, nitrite), phosphorus, and suspended solids (Clark and Siu 2008; Plummer and Long 2007; Viviano et al. 2014). Thus, the utility of the SAWS biofilms' taxonomic data from the current dissertation, much like it is for climate change studies, is the baseline it offers for those investigating the ecological impacts of observed water changes. Whether shifts in biofilm community composition, corresponding to either large-scale climate change or local eutrophication, impact the in situ preservation of SAWSs is unknown. Broaching this question will require the use of future studies, including both on-site sampling and laboratory-based mesocosm experiments, to reveal information on the effect of individual taxon and stressors.

Future Directions

The current taxonomic data for the Hawaiʻi SAWS biofilms suggests some of the microbial conditions observed previously impacting the corrosion of submerged aluminum are present at the four wrecks, including the presence of corrosive metabolite producing SRB. There was, however, no ‘smoking gun’ that conclusively identified MIC as a relevant in situ preservation threat to SAWSs. Studies by Price et al. (2021) and Usher et al. (2014) each demonstrated an association between known biocorroders (e.g. iron-oxidizing Zetaproteobacteria and the methanogenic archaea) and areas of corrosion on steel WWII-era UCH. Taxonomic associations with visible corrosion were not evident for the Hawaiʻi SAWSs, as the bacterial profiles for samples from corroded and non-corroded surfaces were not significantly different.

A negative or inconclusive result regarding MIC does not negate the utility of this research for SAWS management. Rather, the data serves as a launching point for subsequent studies that build of the initial sample collection. The criteria for a MIC diagnosis laid out by Little and Lee (2022) is referenced in Chapter 4, and offers a succinct yet comprehensive overview of the requisite lines of evidence. With over 30 years of experience in researching MIC, the authors’ treatise on the subject serves as a valuable guide for site-specific applications. Instead of repeating their conclusions or abstractly discussing next steps, concrete recommendations for the current study sites are set forth below. This is intended to not only demonstrate the dissertation’s scientific merit but provide UCH managers responsible for SAWSs with ideas for future projects. Communication from the relevant management agencies, chiefly the Hawai‘i State Historic Preservation Division and Office of National Marine Sanctuaries, with the University of Hawai‘i at Mānoa (UH) could increase the feasibility of the proposed research. A local university partner would both eliminate sample shipping costs and significantly reduce risks of sample degradation inherent in long-distance shipping. The latter enables various forms of molecular analyses that may be precluded by substantial lags between collection and processing. The UH Department of Marine Biology department is well-versed in employing microbiological methods to investigate questions related to the intersection of biofilm and the preservation of natural resources (e.g. coral reefs), thus serving as an obvious research ally with the requisite facilities (Hadfield 2011; Huggett et al. 2009; Lema et al. 2019; Remple et al. 2021; Shikuma and Hadfield 2005; Vijayan and Hadfield 2020). Heritage preservation should be conceptualized as an inherently interdisciplinary endeavor that benefits greatly from collaborations and the cross-field exchange of knowledge.

Metagenomic Sequencing and Other Molecular Methods

For an MIC diagnosis three key components need to be identified: corrosion product, corrosion mechanism, and an association between microbes and the observed corrosion (Little and Lee 2022). While each of these were discussed with respect to the current study of SAWSs, a considerable amount of additional work is needed before definitive statements regarding MIC and this site type can be made. This starts with addressing the inability of the microbial community data to convey the functional capabilities of the SAWS biofilms. This information is crucial to discerning potential corrosion mechanisms and associations with specific taxa (Beale et al. 2016; Knisz et al. 2023; Kotu et al. 2019; Procópio 2020; Puentes-Cala et al. 2022).

Replicate samples from the four SAWSs, currently frozen in storage, could be used to rectify this situation by applying metagenomic methods, such as shotgun sequencing, to determine the functional genes present and assess the biochemical reaction potential in these mixed microbial communities. Rather than targeting variation of a single gene (16S rRNA in the current study), shotgun sequencing focuses on short sequence fragments from all genes corresponding to each of the microbes present (Quince et al. 2017). Gene functionality is then predicted and annotated using reference gene databases (e.g. Kyoto Encyclopedia of Genes and Genomes), enabling an evaluation of gene abundances and pathways (Du et al. 2014; Douglas et al. 2020; Kanehisa and Goto 2000). These results are not only used to infer the functions of the individual communities but serve as points of comparisons between contexts (e.g. sites) that can reveal distinct patterns of functional potential.

For UCH management, the analysis of biofilm metabolic potential is most relevant when it can be linked to genetically encoded indicators of MIC. Given the previously-discussed significance of sulfate reduction to increased metal corrosion, dissimilatory sulfite reductase (DsrA, DsrB) genes are often of interest (Krohn et al. 2021; Zhang et al. 2019, 2022). These genes are involved in the final phase of sulfate reduction and production of sulfides (Müller et al. 2015). Similarly, the co-occurrence of genes implicated in aerobic O_2 reduction and anaerobic NO_3 reduction may be indicative of an oxygen concentration cell, and thus, a target for future investigation (Zhang et al. 2022). Gene prevalence within the replicate SAWS biofilm samples can be assessed in a way similar to how the taxonomic compositions of samples were compared by both type, site, and location on a single wreck (i.e. corroded vs. non-corroded). This may yield insights related to the possible corrosion mechanism (e.g. sulfuric metabolites) and associations with bacterial culprits.

Yet, some have suggested that there may not be linear correlations between the severity of corrosion and gene copy numbers. Avelino-Jiménez et al. (2023:4) make the excellent point that “biocorrosion is a complex process where the participation of microorganisms is not limited to a single group, species or environmental condition.” Previous research has revealed that a host of other functional genes, primarily those responsible for hydrogen cycling (hydrogenase and dehydrogenase), are correlated with the MIC of iron (An et al. 2016; Kato 2016; Lekbach et al. 2021; Tsurumaru et al. 2018). Gene enrichments corresponding to increased metal corrosion have been known to correspond with additional influences, including nutrient regimes and hydrocarbon exposure, thus demonstrating the multivariate process involved in MIC (Garrison 2021; Mugge et al. 2019b; Salerno et al. 2018; Zhang et al. 2022). The same comprehensive approach that revealed these connections between microbial gene functionality and iron corrosion are only now being applied to aluminum. To date, no functional genes beyond those involved with sulfate reduction have been proposed as specific indicators of aluminum MIC. There has, however, been the identification of genes that appear supportive of aluminum colonization, such as the methyl-accepting chemotaxis protein-encoding gene (mcp) observed in disproportional abundances within biofilms on non-copper aluminum alloys in Yap Trench (Zhai et al. 2022). Whether this gene correlates to the MIC process or simply facilitates colonization of submerged aluminum remains to be seen.

On-Site Coupon Experiments

The uncertainty regarding genetic markers of aluminum MIC, combined with the innate complexity of the process, necessitates a comprehensive approach that goes beyond in situ sampling. Coupons composed of the same aluminum alloys (e.g. Al 2024) used in aircraft construction can be placed at each of the four sites. The coupons serve as a proxy for the corrosion products associated with the SAWS surfaces, thus negating the need to negatively impact a site by removing corroded elements for analysis. Upon retrieval, the coupons' surface morphology can be assessed using scanning electron microscopy (SEM) to view pitting and other corrosion products (Rodríguez et al. 2002). The latter has also been subjected to various X-ray diffraction and spectroscopic techniques that lead to determinations regarding the chemical species on the coupon surface (Liu et al. 2014; Wang et al. 2020). Corrosion rates can be estimated by equations that incorporate coupon weight loss (ATSM International 2005; Dai et al. 2016). Together, these complimentary forms of analysis work to satisfy the MIC diagnosis requirement of identifying a corrosion product. Without confirmation of on-site corrosion, the taxonomic and genetic data have limited use to decisions regarding the prioritization of in situ preservation threats.

Ideally, multiple coupons would be left at a single site, as it would allow for sequential sampling to determine biofilm succession patterns. Individual coupons can be retrieved at predetermined intervals with the corresponding biofilm communities representing early, middle, and late stage microbial growth (Antunes et al. 2020; Bech et al. 2024; Daille et al. 2023; Li et al. 2022; Summers 2022). Biofilms would be removed and subjected to metagenomic sequencing to determine community composition and functional gene potential. Longitudinal comparisons of both the genetic data and coupon surface morphology should provide insights into how aluminum corrosion is impacted by changes in the biofilm constituents and functional gene abundance. Examples of unique or skewed functional potential between the biofilm communities, as indicated by the enrichment of specific genes, correlated with coupons exhibiting more extensive corrosion would serve as a logical starting point for more targeted investigations. Inter-site comparisons among the four SAWSs would shed additional light on if the microbial succession in Hawai‘i biofilms proceeds in a uniform manner, or if site-specific conditions lead to divergent succession patterns. It is worth noting that the current study's results suggest that any on-site coupon testing should account for the anticipated effect that sedimentary interactions, namely intermittent burial, have on shaping biofilm communities. Thus, researchers should consider a coupon's positioning relative to the seafloor and strive to recreate the conditions most similar to the corresponding wreck.

Mesocosm and other Laboratory Experiments

The value of coupon-based studies lies in the ability to subject a sterilized substrate of interest to the real-world environmental conditions associated with specific UCH sites. There is, however, a near-endless list of documented factors that affect microbial metabolism and growth in marine biofilms contexts. The potential for both confounding and colinear environmental impacts encourages the use of laboratory-based mesocosm studies that enable control over specific variables. Certain experimental work would require the use of locally-available facilities, as proposed by the recommendation for partnering with UH. The practical constraints of the geographical separation between sample sites and the ECU Department of Biology department was, of course, a limiting factor in the scope of the current dissertation. With this impediment resolved, coupon biofilms either formed on site or in laboratory settings through inoculation, could be available for future mesocosm experiments that focus on the taxonomic and functional responses to changing environmental conditions (e.g. temperature, salinity, and available nutrients).

Research has shown that alterations to such variables can impact the MIC process through adaptations that are designed to either mitigate metabolic stress or take advantage of the changing circumstances (Ibrahim et al. 2018; Liu et al. 2017 Ma et al. 2020; Salgar-Chaparro et al. 2020). The example of crude oil exposure's impact on microbial metabolism (e.g. hydrocarbon degradation) and increased corrosion has already been given (Salerno et al. 2018). The biofilm communities associated with substrate samples that demonstrate notable surface morphology impacts can then be subjected to the same metagenomic methods used to identify taxonomic composition and gene abundance. Yet, Krohn et al. (2021:8) has highlighted that "metagenome-based studies only describe the genetic potential," thus leaving a void regarding which genes are actually being expressed. For this information, RNA sequencing has been promoted as a way of discerning which of the genes are most transcribed (i.e. active) (Gomes et al. 2023; Ozsolak and Milos 2011; Van Vliet 2010). The collection and isolation of RNA is often prone to contamination and sample degradation (Imdahl and Saliba 2020; Lu et al. 2022). Thus, experimental biofilms grown in laboratory conditions, as opposed to those collected in situ, are most suitable for sample collection and processing. The transcriptional data can be used to answer questions related to the most prominently expressed genes, the primary metabolic pathways being utilized, and which bacterial species are most transcriptionally active (Choi 2016; Croucher and Thomson 2010; Han et al. 2015). When metagenomics are combined with transcriptional studies, a deeper understanding of the connection between observable corrosion and the various factors that influence gene abundance and expression is made possible (Beale et al. 2016; Knisz et al. 2023; Krohn et al. 2021; Puentes-Cala et al. 2022).

In some cases, MIC is not intrinsically linked to a specific metabolic pathway, but instead correlated with a general increase in microbial activity, as suggested by Melchers (2014). The situation is further convoluted by difficulties in discerning between the impacts of biological and chemical corrosion, with biotic and abiotic factors sometimes combining to increase metal degradation. To confront this issue, measurements of cell activity (e.g. ATP, ADP, and AMP) utilizing luminescent reaction methods has been proposed as a possible indicator of MIC. Specifically, experimental biofilms corresponding to observed (e.g. SEM) coupon corrosion can be assessed in terms of their metabolic rates (Salgar-Chaparro et al. 2020). Activity and the associated effect on corrosion can then be reassessed following experimental treatments (e.g. nutrient enrichment). It is important to not only understand the microbes and the specific genes involved in MIC, but also the stimuli that could create the requisite conditions for this complex process. Whether using taxonomic composition, functional gene profiles, or cell activity, it is also imperative that these biological lines of evidence are tracked in parallel with quantifiable measurements of corrosion in response to the variable manipulation. This enables site managers to both evaluate the current potential of MIC and anticipate the likelihood this changes as natural and anthropogenic influences alter the marine environment.

As evidenced by the current data for the SAWSs, the microbial consortium of marine biofilms can be highly diverse, making identifications of specific microbial taxa as contributors to the MIC process difficult. Community composition and functional gene profiles of in situ and lab-based samples can be used to infer associations between certain microbes and corrosion, while also identifying potential corrosion mechanisms. To further pinpoint specific taxa and test the presumed corrosive effects, researchers have cultured isolated strains of suspected biocorroders and performed growth experiments on the substrate of interest (Lu et al. 2023; Price 2020; Qui et al. 2009; Zhang 2022). For the Hawai‘i SAWSs, the *Desulfobulbaceae* stands out as a potential bacterial family from which culturable strains could be isolated. As has been done in previous studies, growth of these SRB on the aluminum surface can be measured (e.g. most probable number or optical density methods) in conjunction with metabolite (e.g. sulfite) concentrations and documentation of surface morphology impacts (Guan et al. 2017, 2020).

Correlation between these three lines of evidence could be used to support conclusions regarding the MIC capabilities of specific taxa, who would then be further investigated.

Additional Lines of Evidence: Electrochemistry

Though the focus has been on the microbiological aspect of SAWS corrosion, the actual process of aluminum corrosion is an innately electrochemical one tied to oxidation and reduction reactions (Blackwood 2018; Dexter 2002; Little and Lee 2014; Little et al. 2020). As Knisz et al. (2023:20) points out "[n]umerous EC techniques have been developed to mechanistically study fundamental corrosion mechanisms in the laboratory, in addition to monitoring corrosion behavior in field conditions." Many of these techniques are outside the realm of microbiology, thus inviting UCH managers to seek out further interdisciplinary collaboration with experts in electrochemistry. To better elucidate insights into the effect microbes have on the corrosion process, assessments of corrosion and surface morphology via microscopy can be supplemented with electrochemical measurements of corrosion potential (E_{corr}) and pH. The latter form of survey can be used to track the inferred rate of corrosion for both the four SAWSs, as well as aluminum coupons subjected to various experimental treatments. The extent of corrosion is not only discerned using optical methods, but also empirically quantified.

The longitudinal work conducted by Vicki Richards and Jon Carpenter in Saipan, which was referenced in Chapter 1, offers an excellent example of corrosion monitoring applied to SAWSs. From 2012-2023, the corrosion potential and pH of aluminum surfaces for several SAWSs off the coast of Saipan were measured and plotted on an aluminum-specific Pourbaix diagram (Richards and Carpenter 2012, 2018; Pruitt and McKinnon 2024). While the data from the 2023 collection is still being processed, a comparison of 2012 and 2017 observations revealed that the majority of aircraft were in a passive state of corrosion, with aluminum oxide as the dominant product (Richards and Carpenter 2018). Though no statistically-significant changes were recorded, a general increase in both the Ecorr and pH values suggested that corrosion rates may actually be decreasing due to the protective oxide layer, which was especially pronounced for sites in shallower, more oxygenated environments. Additionally, the corrosion mechanism also appeared to be changing owing to the galvanic corrosion of aluminum components comprised of different alloying constituents being in electrical contact. The use of various aluminum alloys in WWII aircraft construction, however, complicated straightforward interpretation of the electrochemical data (Ouissi et al. 2019). Copper, of course, was the main alloying component for Al 2024, though iron, magnesium, manganese, and zinc were also utilized. The incorporation and percentages used of these different alloying metals changes the corrosion potential of the metal (Davis 1999; Reboul 1979; Sukiman et al. 2012; Zhu et al. 2023). The more reactive alloys consisting of zinc and magnesium likely provide a form of cathodic protection for the less reactive aluminum-copper parts (Féron 2007; Ghali 2010; Reboul 1979). In turn, the latter may preferentially corrode when in contact with more noble metals, such as the steel engine. Only one plane yielded an increased corrosion rate (Consolidated PB2Y Coronado), which was attributed to the site's disarticulation, and thus, a lack of electronically-connected components capable of offering cathodic protection.

Richards and Carpenter (2018) provide a thorough description of the survey methods, which has been summarized here. The pH measurements can be taken by a pH electrode/meter assembly, while corrosion potentials are measured using a platinum electrode connected to digital multimeter and reference electrode. Both meters should be placed in a waterproof housing capable of withstanding water pressures associated with site depths. Richards and Carpenter (2018:4) reported that the "measurement of pH on the aluminium alloy aircraft surfaces was difficult owing to the very thin layer, often less than 1 mm, of marine growth and corrosion products," which resulted in more conservative pH data and likely an underestimation of the wreck surfaces' acidity. In recording the electrochemical data, the biofilm layer is scraped away and the pH electrode is pressed flush against the newly-exposed, metallic surface. Immediately after the pH is recorded, the platinum electrode is inserted, with good electrical contact indicated by stable voltage as measured against the reference electrode. Other key environmental parameters that can inform interpretations of the electrochemical data, including the temperature, salinity, dissolved oxygen, pH, and redox potential of the ambient seawater, can also be measured using cable-connected sensors. For the Hawai'i SAWSs, the initial electrochemical measurements are needed, as they not only provide a baseline for subsequent comparisons, but using the results from Saipan as analogs is likely inappropriate due to differences between the oxidizing marine environments. Just as microbial responses to temperature and pCO2 increases are community dependent, interpretation of a site's corrosion potential and pH, also appears to be location-specific.

Neither the physical equipment, nor the recording methodology are overly complex or expensive. Together, these make electrochemical surveys a viable monitoring technique for UCH management agencies and should be incorporated into best management practices. Interpretation of the data and calibration of the recording electrodes, however, does necessitate a certain level of expertise. Similar to mixed alloy use, microbial biofilm, the "musciligous layer" observed by Richards and Carpenter (2012, 2018), also complicates interpretation of the electrochemical data and may prevent definitive statements regarding site deterioration. In fact, it is the inability of corrosion potentials and pH to convey the totality of SAWS corrosion that served as the catalyst for the current dissertation. The cathodic protection referenced earlier is a result of more noble (less reactive) metals in contact with less noble ones. Biofilm, however, is also known to influence metallic corrosion rates through the ennoblement of surface metals (Eashwar et al. 1995; Johnsen and Bardal 1985; Little et al. 2008, 2013). Thus, it is difficult to determine if the more electropositive (i.e. increased) corrosion potentials, indicative of lower corrosion rates, is a biological or electrochemical phenomenon (Knisz et al. 2023; Little and Wagner 2001). Research using aluminum corrosion potentials and SRB biofilms revealed initially low values, correlating to increased corrosion rates, before potentials shifted to more electropositive for the remainder of the experiment (Guan et al. 2020). The relatively high level of susceptibility to corrosion was eventually replaced by lower metal loss and higher corrosion potentials, suggesting the biofilm provided a protective barrier for the underlying aluminum. The corrosion-inhibiting role of biofilm has been noted for other studies of submerged aluminum (Gao et al. 2021; Guan et al. 2020; Mansfeld et al. 2002; Örnek et al. 2002; Shen et al. 2020**)**. Additional research studies aimed at discerning the effect biofilm has on electrochemical parameters of corrosion would greatly benefit interpretations of the E_{corr}, pH, and biological data in terms of relevance to site corrosion.

Additional Lines of Evidence: Photogrammetry

For UCH managers, the potential or theoretical existence of corrosion is of concern when it corresponds to actual site disarticulation and metal loss. Since wreck elements cannot be examined in the same way test coupons can, using SEM imaging and other laboratory-based techniques, alternatives for capturing corrosive impacts must be considered. As posited elsewhere in this dissertation, photogrammetry, the overlapping of images in order to create a single digital object, represents a valuable resource for this pursuit. A solitary 3D model may help visualize the current status of a SAWS, but longitudinal comparisons via points-based deviation analysis allow for quantifiable assessments (Cvetkovic 2020; Rossi et al. 2019; Yamafune 2024). The repetitive photogrammetric recording of the same wreck can generate georeferenced-point cloud datasets. Using CloudCompare software, the individual distances between points for these point cloud datasets can be expressed as color-scaled heatmaps that highlight the greatest areas of change (Holst et al., 2017; Neuner et al., 2016; Schroeder and Klonowski 2019). Rossi et al. (2019:56) concluded that "'deviation analysis' based on photogrammetry could track changes on underwater sites over time, and could be used for site management plans."

The feasibility of this monitoring strategy has been greatly increased by the advent of action cameras (e.g. GoPro) and acrylic dome housings. The production of high quality, accurate photogrammetric models is no longer dependent on expensive DSLR cameras and complex underwater housings. Calibrated GoPro cameras, situated within inexpensive dome housings to counteract the magnifying effect of the water, are a more than adequate solution to budget constraints that negate the use of costly photographic equipment. Swimming in predetermined patterns, as described elsewhere, a diver (or team of divers to mitigate air use and decompression limitations) can obtain thousands of overlapping photos on a single dive. Characterized as a form of rapid site assessment, repeated photogrammetric recording supplements traditional archaeological documentation that relies on hand measurements and baseline offsets (Bush et al. 2023). While the latter is undoubtedly beneficial, the time commitment involved often makes it impractical for management agencies to perform on a regular basis. Each 3D model and point cloud becomes legacy data for which future recordings can be compared against to track site degradation over time. The affordability of this method may be somewhat offset by the licenses required for the photogrammetry software. In such cases, managements agencies on site may again look to partner with academic institutions who have the requisite licenses. Photographic data can be gathered during short (~1 hour) site visits and then later shared. For the current study, 3D models were generated for three of the sites, with each made publicly available for viewing on Sketchfab.[1] The data itself (photos, point clouds, etc.) is available upon request for the relevant management agencies (e.g. Hawaiʻi SHPD, NOAA ONMS, NHHC).

Ultimately, maximizing the utility of the photogrammetric data for understanding processes of MIC will depend on its integration with the biological and electrochemical observations. It is easy to imagine a scenario where a future photogrammetric recording of a site (e.g. Oʻahu Thunderbolt) reveals significant degradation via point cloud deviation analysis. The impacted area would inform site managers on where to prioritize both biofilm sampling and electrochemical testing. The former, using the methodology prescribed here, offers a look at the potential microbes and functional genes that may be impacting corrosion. Additionally, the taxonomic data can be compared with the results of the current study to determine if any significant changes in community composition have occurred. Confirmation of whether these changes are contributing to the observed corrosion will require onsite and mesocosm coupon experiments focused on biofilm development, the extent of superficial corrosion, and bacterial responses to different stressors. The biological interpretations can be paired with the electrochemical readings of the wreck components in question. Comparisons of the latter with measurements yielded by areas that appear uncorroded would then be used to infer the possibility of increased corrosion rates and make determinations regarding the corrosion mechanism. If the separate, but complimentary lines of evidence support an MIC diagnosis, there may be several mitigation strategies available.

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[1] https://sketchfab.com/bushd16

Possible Forms of Mitigation

Before discussing the various options for combatting the effects of MIC on SAWSs, site management decisions require the consideration of numerous cultural, economic, and practical aspects. Just because a form of treatment is possible, it does not mean it is advisable. In some situations, acceptance of decay and site loss may be an acceptable form of in situ preservation given the tradeoffs between resource expenditures, historic significance, and stakeholder interest. For WWII SAWSs, whose importance to the heritage tourism industry, national identity, and local ecology has been discussed, more involved methods of intervention may be warranted. This is made especially true by the threatened supply of in situ SAWSs, as salvaging, both legal and illegal, increases throughout the world's oceans. Rather than covering the full gamut of in situ preservation actions at the disposal of UCH managers, as was done in Chapter 1, the following will briefly overview proposed forms of mitigation specific to MIC. Of course, the necessity of mitigating MIC is unknown, and will only be revealed after determining the exact relevance of MIC to SAWS deterioration. There is little sense of fixating on cures for a problem that may not exist. However, if MIC is eventually revealed, through the interdisciplinary approach advocated for here, to be a significant contributor to SAWS loss, managers are not necessarily powerless. Thus, the possibility of mitigation serves as a justification for the investment in research that furthers the understanding of MIC impacts on historic preservation, in an attempt to be more proactive about site management.

In aviation and marine engineering, organic (isothiazolone, quaternary ammonium, and aldehydes) and inorganic (e.g. ozone, chlorine, and bromine) compounds have proven capable of reducing or preventing microbial cell activity on and within the surfaces of contemporary aircraft parts (Lee et al. 2010; Nelson et al. 2017; Oguzie et al. 2012; 2013). Similarly, Angarano et al.

(2007) note that natural antifouling biocides (e.g. capsaicin) have the added benefit of being an environmentally-friendly option. From within the field of archaeology, Yin et al. (2019) discovered possible MIC culprits associated with wooden dishes from a shipwreck off the coast of China. Cultured communities generated from the dishes were subjected to four types of biocides in hopes of identifying a taxa-specific solution to issues of MIC. Another possible option is discussed by Kurzbaum et al. (2019), who made the point that leather in underwater archaeological contexts often is devoid of biofilm deposits due to the effects of certain polyphenols (e.g. tannic acids) and proteins on leather surfaces. This sort of antifouling substance can prevent the adhesion of bacteria and inhibit their growth. Kurzbaum et al. (2019) argue that using coating treatments comprised of similar compounds could be applied to the surface of submerged wrecks, although this requires more information on the specifics of microbial communities. Finally, it may eventually be proven that the promotion of certain corrosion-inhibiting microbes, rather than only preventing or neutralizing microbial activity, could be a viable solution (Kip and Van Veen 2015; Ornek et al. 2002). The practicality of using biocides and other treatments in underwater contexts will be challenged by difficulties related to biofilm penetration and the diffusive effects of water.

These chemical treatments are, of course, in addition to previously-mentioned forms of in situ preservation, including site reburial, sacrificial anode use, and relocation. The appropriateness of both chemical and non-chemical mitigation methods will depend on experimentation and analysis that targets site and taxa-specific solutions. What may work for one site, given the microbiological and physical conditions, may be counterproductive at another site. Determinations of treatments will also need to consider more practical aspects related to cost and stakeholder demand that are inherent in all site management decisions. The field of UCH management, however, is still years away from this step of in situ preservation of WWII SAWSs. For now, managers and researchers should continue to concentrate efforts on better understanding the associations between microbial diversity and active corrosion of wreck sites through consultation with subject matter experts in microbiology and electrochemistry. By answering the questions of ‘who’ may be contributing to MIC and to what extent is this affecting site preservation, site managers can eventually focus on the all-important question of ‘how’ as it pertains to inhibiting MIC. Thus, information is the best tool for site manager currently considering the impacts of MIC. By having a complete picture of the decay forces, including non-deterministic ones, such as MIC, in situ preservation can proceed in a more informed manner. Decay trajectories and models are more accurate with MIC data incorporated, which allows for more opportunities to select timely and appropriate mitigation strategies.

Final Conclusions

Over 80 years ago, WWII transformed the Hawaiian Islands from a remote territorial outpost of the US to the country’s strategic center of wartime operations in the Pacific. Perhaps no single symbol better embodies the archipelago’s rapid militarization than the aircraft that once filled the skies. Newly-minted aviators received vital training in Hawai‘i, learning dive-bombing, combat formations, and anti-kamikaze tactics, among other invaluable skills. The practice flights provided life-saving experience from which aircrews could draw upon when deployed to the frontlines. However, danger and mishaps were not exclusive to the forward operating areas. Issues pertaining to inexperience, experimental technology, foul weather, and, of course, the occasional ‘gremlin,’ resulted in over 1,000 planes reportedly crashing in the waters around Hawai‘i. These wrecks, which have occasionally involved the loss of human life, now constitute a significant portion of the islands’ submerged cultural landscape. While only a fraction of the aircraft that are recorded as wrecking in Hawaiian waters have been located, several of those that have been relocated now serve as popular recreational sites, including two investigated in this study. Site visitors are drawn by a diversity of motivations, ranging from interests related to the aircraft's historical and cultural significances, to more leisurely pursuits associated with wreck diving and artificial reefs. Yet, the snorkelers and SCUBA divers that physically interact with these wrecks are by no means the sole stakeholders. Many of the same qualities that drive site access are responsible for fostering a sense of reverence amongst the public, the majority of which will never swim alongside the SAWSs. The US historic preservation laws have codified this desire for safeguarding WWII aircraft, with legislation specifically aimed at sunken military craft.

In Hawaiʻi, SAWS management is a collaborative responsibility that is largely shared by the SHPD and the NOAA ONMS, through legal jurisdiction established by the National Marine Sanctuaries Act. At a more general level, the NHHC has been tasked with the mission of protecting naval heritage and naval properties, thus serving as the chief administrative body for regulating actions that affect military SAWSs. Together, the site stewardship entrusted to these agencies is a form of public good, where tradeoffs and competing objectives are factored into management practices. Considerations of resource expenditures, potential economic consequences, and historical significance are used to rationalize decisions regarding how to best maintain a representative sample of Hawaiian and US military history. From a management perspective, in situ preservation has often been touted as the preferred option, given its practicality, site access benefits, and international agreements regarding the efficacy of this strategy. However, warbirders and other salvors motivated by the commodification of WWII aircraft have placed increasing pressure on the field of archaeology to justify in situ preservation.

Proponents of SAWS recovery, who have been further empowered by recent actions regarding the USN's Trade and Exchange Program, often associate in situ preservation with inactivity and a lack of interest in protecting the resource. Whether it is arguments made before military officials, or blog posts intended to sway the court of public opinion, allowing the SAWSs to remain in place has been incorrectly conceptualized as accepted site loss. Proposals to recover aircraft remains from aquatic contexts, which are likely to become increasingly marine focused, are presented as a proactive form of management that preserves wartime vestiges for future generations. Decades of shady salvage efforts should motivate archaeologists to be prepared to refute these claims and justify in situ preservation as the preferred alternative to recovery.

Of the site transformation processes that are mentioned as justifications for SAWS recovery, corrosion has garnered the most attention. Those that seek to challenge the merits of in situ preservation appear to assume that the corrosion of aircraft sites will lead to their inevitable disappearance. These arguments, while potentially valid, are most often made with little to no scientific evidence. Without data regarding corrosion rates and mechanisms, counterpoints to the salvor perspective are left equally uninformed. Archaeologists and site managers should be able to speak to critical points of site corrosion: 1) to what extent is corrosion occurring?; and 2) can the corrosion be mitigated? The answers to both are inherently interdisciplinary as corrosion, as well as its inhibition, relies on electrochemical processes that are influenced by a lengthy list of biotic and abiotic factors. The scientific complexity of corrosion necessitates collaborations with subject matter experts beyond archaeology and the employment of research methods borrowed from other disciplines. It is in this spirit that the current dissertation sought to contribute to the fields of underwater archaeology and cultural resource management by considering and analyzing the potential role microbes play in the corrosion of SAWSs.

Current Understanding of the Relevance of Microbiologically-Influenced Corrosion to Submerged Aircraft Wreck Site Management

Today, economic damages incurred through MIC are estimated to be in the billions (USD) worldwide, with most of that valuation stemming from impacts to oil and gas infrastructure (Little et al. 2014; Yazdi et al. 2022). Justifiable concerns regarding MIC has spurred decades of research efforts to understand the biotic and abiotic factors that promote MIC, which reveal a truly complex and interconnected web of influences. This is especially true for marine contexts, where inherently dynamic biofilm communities are subjected to natural and anthropogenically-induced changes. Recognition of this threat to submerged metals led to the consideration of the effects MIC have on UCH resources, specifically steel shipwreck sites. While investigations into the interactions between microbes and the sunken vessels they colonize yielded a wealth of knowledge regarding the marine microbiota's role in historic preservation, this line of research had not been extended to SAWSs, until now. The current dissertation represents the first attempt to characterize the microbiome associated with this site type, and thus, intended to ignite critical discussions pertaining to the relevance of MIC to SAWS management.

While the taxonomic data obtained from the four SAWSs in Hawaiʻi did not directly reveal the relationship between site corrosion and microbial presence, there were findings that advance the understanding of how microorganisms may affect in situ preservation. First and foremost, the DNA sequencing results indicated that each site possessed unique and diverse biofilm communities. The bacterial composition of these communities was irrefutably distinct from that of sediment and seawater samples. The diversity of microbes is highlighted by a co-occurrence of aerobic and anaerobic microbes, which suggests that there may be oxygen gradients within the biofilm layers. Differential oxygen levels and the uneven distribution of biofilm on a metal surface are the two requisites for an oxygen concentration cell. The juxtaposition of oxygenated and deoxygenated surface areas, as is made possible by biofilm, is known to increase the rate of corrosive redox reactions. The anaerobic biofilm constituents for all four sites included SRB, who are often cited as the archetypal MIC culprit due to their production of sulfuric metabolites. These bacteria are frequently observed within marine sediments, as was true for the sediment samples from the four Hawaiʻi SAWSs. However, the SRB assemblages produced by biofilm samples differed considerably from that of the sediment samples. This remained true for all four sites, with biofilm SRB abundance appearing uncorrelated with sediment SRB abundance.

Though the data indicated that certain conditions for MIC are possible, this does not equate to the occurrence of MIC as being plausible. Identification of an oxygen concentration cell cannot be accomplished on taxonomic data alone, while laboratory experiments from studies outside of the historic preservation field indicate that SRB presence on submerged aluminum can have mixed impacts for corrosion (e.g. Guan et al. 2020). Thus, the exact relevance of MIC to SAWS management has not been answered by this dissertation. This does not mean the data does not have value. As the initial sampling effort, the microbial profiles for each wreck serve as a baseline for subsequent comparisons. Future site assessments may reveal instances of considerable degradation. The change in a site's physical condition can be considered in relation to changes in the microbiome. Additionally, high sample counts and inter-site comparisons for the current study allowed for inferences regarding the influences that shaped the composition of these communities. While some similarities are shared between the wreck biofilm samples and previously-analyzed aluminum biofilms, the local environment appears to be the dominant factor. Bacterial assemblages associated with the SAWSs were taxonomically similar to several others reported for marine biofilms in Hawaiʻi (e.g. Lema et al. 2019; Vijayan and Hadfield 2020). The latter consisted of non-aluminum substrates, including glass slides and corals, thus indicating that substrate material may not be as influential as expected.

Environmental impact on wreck biofilm communities is further evidenced by the relatively high level of congruency shared by wrecks from different islands. The biofilm samples from the Hellcat and Corsair sites exhibited taxonomies consistent with a sedimentary influence corresponding to intermittent burial. Conversely, the Helldiver and Thunderbolt biofilms reflect a higher contribution of bacteria associated with free-floating, planktonic communities. These initial inferences regarding the interplay of environmental microbiomes and SAWS biofilms can be used to anticipate and assess future changes. For example, the responsive nature of the biofilm communities to the surrounding environment suggests that shifting ocean conditions linked to local pollution (e.g. eutrophication) and larger-scale climate change (e.g. ocean warming and acidification) will correspond in taxonomic changes. Whether these changes have any connection to MIC and increased site degradation remains to be seen. Yet, without the initial baseline data, answering that question is impossible. Similarly, the data may be of use to scientists outside of historic preservation who are interested in examining the effects anthropogenic activities have on the local ecology. Biofilms have been used in the past to explore coral larva settlement, biodiversity monitoring, and marine carbon cycling. The preliminary characterization of the wreck biofilm communities can assist these non-archaeological pursuits through the interdisciplinary transfer of knowledge. Of course, the results are not the only useable aspect of this project. The sampling methodology was found to be cost-effective, minimally-intrusive, and capable of creating the current dataset. High success rates of DNA extraction and sequencing attest to the collection method’s efficacy in obtaining biofilm samples from SAWSs. The methodology can be utilized by subsequent SAWS biofilm studies in Hawai‘i and abroad that take aim at discerning MIC impacts and the role of SAWSs as artificial reefs. Additionally, the syringe method presented here may be of use to other research endeavors that involve the collection of biofilm from artificial surfaces at diver-accessible depths.

Value of Current Study to Submerged Aircraft Wreck Site Managers

Though the current study yielded an inconclusive result regarding the relevancy of MIC to SAWS preservation and management, there is still value in the ignition of conversations surrounding the topic. The concept of MIC was first described by Gaines (1910), yet, it was not applied critically to UCH management until the late 1980s, when concern arose over the potential corrosive impact rusticle formation had on RMS *Titanic*. The seven-decade lag has since been compensated for by a multitude of informative studies that assessed how microorganisms affect submerged sites, mainly steel shipwrecks (Albahri et al. 2019; Church et al. 2007; Cullimore and Johnston 2008; Damour et al. 2016; De Baere et al. 2019, 2021; Little et al. 2019; MacLeod et al. 2017; Mugge et al. 2019a; Price et al. 2021; Salazar and Little 2017; Van Landuyt et al. 2022). Examining the intersection of marine biology and underwater archaeology is now far from a radical concept, the merits of which appear to be no longer in question. The phrase ‘shipwreck ecology’ is becoming an increasingly common one in the lexicon of the discipline, with publications dedicated to the topic (Hickman et al. 2023; Meyer-Kaiser et al. 2022; Paxton et al. 2024). It is difficult, however, to ignore the exclusion of non-shipwreck resources by this terminology.

While the difference may be an unintentional, semantic one, it does mirror the overall trajectory of WWII aircraft as archaeological resources. For years after the war, professional historic preservationists ignored crash sites, as amateur aviation archaeologists salvaged what they could (Fix 2011). The conceptualization of aircraft as historic resources changed in the final decades of the 20th century. Conversations concerning the cultural significance of WWII planes and how the crash sites can yield pertinent archaeological information led to a general acceptance of these aircraft within the purview of archaeology (Cooper 1994; Jung 1996, 2008; McCarthy 1997; Rodgers et al. 1998; Spennemann 1998). Just as shipwreck ecology as a subdiscipline has recently manifested, so has aviation archaeology, with a recent attempt to define a standardized approach to the archaeological investigation of aircraft (Whitehead and Lickliter-Mundon 2023). The current dissertation, thus, extends efforts in developing aviation archaeology methods to include considerations of wreck ecology that were recently expressed by Paxton et al. (2024). The microbial data from the Hawai‘i SAWSs suggests this conversation is warranted. The NHHC has concurred, voicing both interest and support for future microbiological studies in response to the Special Use Permit Report submitted for the Corsair site.

The genesis of this study was perhaps naïve, in that the original research proposal suggested simple taxonomic associations could reveal proof of MIC. The microbial data quickly debunked this assertion, as evidenced by the lack of significant differences between the community composition of biofilms from corroded and non-corroded wreck surfaces. This negative result, however, should not be viewed as a failure. Instead, the lack of identifying a conclusive link between biofilm taxonomy and corrosion using the current approach informs researchers on what needs to be accomplished next. Corrosion science, especially as it relates to UCH management, should be an iterative process where research methods are built, tested, refined, and improved upon. Speculation on how this can be achieved, in light of the current data, directly led to considerations of what additional lines of evidence are essential to making an MIC diagnosis. The recommendations for metagenomic sequencing, mesocosm experiments, and aluminum coupon studies constitute concrete actions that can be taken to ensure that utility of this research is maximized for those managing SAWS in situ preservation. That said, the first step is still required, and that is truly what this dissertation represents. Rather than continuing to list MIC as a potential, yet unexplored preservation threat to SAWSs, the current study approached the subject in an analytical manner through the characterization of the site microbiomes. While it is now abundantly clear that this is insufficient to make conclusive statements regarding SAWSs and MIC, the foundation has been laid for future studies to build upon the current results.

Detection and treatment methods for MIC in the fossil fuel, aviation, and marine infrastructure industries were formed following similar trajectories of preliminary investigations eventually leading to proposed solutions (Achinas et al. 2020; Fischer 2013; Fischer et al. 2014; Grzegorczyk et al. 2015). The hope that this can be achieved for the MIC of SAWSs will require the same amount of scientific experimentation and analysis that preceded the development of reliable mitigation measures in other fields. In the end, the application of MIC research to SAWSs may yield conclusions that microbial activity is not a significant contributor to the corrosion process. Such a finding should be seen as a success, rather than a waste of time and resources. Not every result related to site preservation threats has to signal the proverbial ‘doom and gloom.’ Determinations of relevance helps site managers prioritize threats and be less concerned with unknowns that were previously characterized as potential factors. The hypothetical lack of evidence for MIC impacting SAWSs would provide additional counterpoints to unfounded accusations of unmitigated site loss as a result of an aircraft’s submergence. The

SAWS electrochemical measurements gathered by Richards and Carpenter (2012, 2018) serve as an example of how empirical data, which indicated a decrease in corrosion rates for most of the sites, can be of value, even if that is to say that the sites do not currently face high risks of environmentally-induced degradation.

Biggest Threat to Historic Submerged Aircraft Wreck Sites?

The interrelated fields of underwater archaeology and cultural resource management are likely years away from definitively answering questions regarding the relevance of MIC to SAWSs. In the meantime, efforts are best spent gathering baseline data, both of the microbiological and electrochemical varieties. The utility of the datasets has been speculated upon and will likely serve as important points of comparison for tracking changes in site condition with changes in site microbiomes. There are, of course, uses for this data that extend beyond the immediate concerns regarding SAWSs, including assessing the ecological impacts of climate change and anthropogenic eutrophication. Rapidly advancing technology, combined with an ever-growing body of knowledge regarding marine biofilms, will likely result in uses of the data not yet considered. Thus, the investment in this foundational step is likely to yield additional research benefits that justify the current study. Perhaps, other institutions and historic preservationists will join the effort to discern the impact microbes have on SAWSs, leading to geographical comparisons between sites in different marine environments.

Yet, the most immediate need for SAWS management is continued documentation of site changes, both gradual and acute. Three-dimensional photogrammetry offers a now affordable and easy way of achieving this goal, with point cloud deviation analysis constituting an empirical method of expressing wreck impacts. Management agencies can further advance these efforts by partnering with site stakeholders, such as the recreational dive community, who have a vested interest in site preservation, as well as universities that have access to the requisite software. Expanding the responsibility of stewardship beyond the agencies legally tasked with historic preservation helps to foster a sense of ownership amongst site visitors. Furthermore, partnerships help raise public awareness of the resources themselves, especially when the aircraft are contextualized with the proper archaeological information and historical significance. In turn this has been proven to increase voluntary compliance, where communities and site users feel an obligation to protect a site for future generations. Site assessments via photogrammetry not only inform managers on possible in situ preservation strategies, but can serve as a visual record that can be used to dispel unfounded and alarmist assumptions of site degradation.

After 80 years, the WWII SAWSs of Hawaiʻi remain in place, evidently capable of withstanding the decades of environmental impacts, including microbial colonization and seawater-induced corrosion. The Maui Helldiver site represents one of the premiere examples of a SAWS in the Pacific, doubling as a testament to the durability of the aircraft's physical remains. This site, and the other three examined in this dissertation, have likely reached a quasi-equilibrium with their marine surroundings, as rapid, unchecked deterioration would have led to their disappearance years before the current study. Thus, as it stands now, the most immediate threat remains salvaging. This appears to be a preservation threat that is particularly applicable to WWII aircraft, as they have been conceptualized by the warbirder community as a commodified collectable. Rationale for recovery and salvage of SAWSs can range from reasonably good intentions related to public displays to less savory, profit-driven motivations. The end results often include a complete destruction of the original aircraft, restored composites built of original and replacement parts, missing historical context, poor conservation practices, and site loss that far exceeds anything currently observed for in situ SAWSs. The best way to combat undesirable recovery operations is garnering support for both in situ preservation and legal protections outlawing salvage. Accomplishing this objective will likely require that site corrosion is demonstrated to be either currently kept in check or it can be mitigated through passive and active forms of stabilization. This perspective is reliant upon studies such as this, and more importantly, research that improves on the current study, in which site corrosion and proposed solutions are empirically assessed.

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Appendix A: Full Sample List

The following is a complete list of samples, including those that failed to sequence (as symbolized by '**'). The "IMR Name" refers to the name given to the samples by the Integrated Microbiome Resource during the sequencing process, while the "Sample ID" refers to the sample name given during collection. The total amount of water filtered in mL is given for each seawater sample.

IMR Name	Sample ID	Sample Type	DNA Concentration (ng/µL)	Description	Depth (m)
DB01	#1	Biofilm	5.25	Hellcat, near non-corr.	9.8
DB02	#2	Biofilm	4.18	Hellcat, near corrosion	9.5
DB03	#3	Biofilm	9.06	Hellcat, near non-corr.	9.6
DB04	#4	Biofilm	7.12	Hellcat, near non-corr.	10.1
DB05	#5	Biofilm	5.65	Hellcat, near corrosion	9.5
DB84	#6	Biofilm	19.80	Hellcat, near corrosion	9.5
DB07	#7	Biofilm	15.10	Hellcat, near corrosion	10.1
DB08	#8	Biofilm	3.19	Hellcat, near corrosion	9.8
DB09	#9	Biofilm	4.44	Hellcat, near non-corr.	10.1
DB10	#10	Biofilm	4.20	Hellcat, near non-corr.	9.8
DB85	Tire	Biofilm	2.01	Hellcat	10.1
DB12	S.S.	Biofilm	1.38	Hellcat	10.1
DB13	#21	Biofilm	11.40	Helldiver, near non-corr.	15.9
DB14	#22	Biofilm	4.80	Helldiver, near non-corr.	15.9
DB15	#23	Biofilm	2.67	Helldiver, near non-corr.	15.9
DB16	#24	Biofilm	9.38	Helldiver, near corrosion	16.2
DB17	#25	Biofilm	12.50	Helldiver, near non-corr.	15.5
DB18	#26	Biofilm	2.45	Helldiver, near corrosion	16.2
DB19	#27	Biofilm	9.43	Helldiver, near corrosion	15.9
DB20	#28	Biofilm	5.47	Helldiver, near corrosion	15.9
DB21	#29	Biofilm	4.87	Helldiver, near non-corr.	15.9
DB22	#30	Biofilm	3.47	Helldiver, near corrosion	15.9
DB23	S1	Sediment	1.44	Hellcat, near non-corr.	10.1
DB24	S2	Sediment	2.64	Hellcat, 5 m away	10.1
DB86	S3	Sediment	12.70	Hellcat, near corrosion	10.1
DB26	S4	Sediment	2.80	Hellcat, green algae	10.1
DB87	S5	Sediment	6.89	Hellcat, 30 m away	10.1
DB88	S6	Sediment	2.96	Helldiver, near non-corr.	16.5
DB29	S7	Sediment	2.13	Helldiver, near corrosion	16.5
DB30	S8	Sediment	1.06	Helldiver, under	16.5
DB31	S9	Sediment	5.08	Helldiver, 5 m away	16.5
DB89	S10	Sediment	2.43	Helldiver, 30 m away	16.5

DB33	W1	Water Filter	8.11	Hellcat	0.3
DB34	W2	Water Filter	10.60	Hellcat	0.3
DB35	W3	Water Filter	14.20	Helldiver	0.3
DB36	W4	Water Filter	15.20	Helldiver	0.3
DB37	W5	Water Filter	15.20	Hellcat	0.3
DB38	W6	Water Filter	18.80	Helldiver	0.3
DB39	Sponge #1	Biofilm	1.14	Hellcat	10.1
DB40	Sponge #2	Biofilm	3.83	Hellcat	10.1
DB41**	Sponge #3	Biofilm	0.07	Hellcat	10.1
DB50**	DB50	Biofilm	1.04	Corsair, near non-corr.	7.6
DB51	DB51	Biofilm	27.00	Corsair, near corrosion	7.6
DB52	DB52	Biofilm	8.49	Corsair, near corrosion	7.6
DB53	DB53	Biofilm	8.51	Corsair, near corrosion	7.6
DB54	DB54	Biofilm	25.80	Corsair, near non-corr.	7.6
DB55	DB55	Biofilm	14.40	Corsair, near non-corr.	7.6
DB56	DB56	Biofilm	2.36	Corsair, near non-corr.	7.6
DB57	DB57	Biofilm	6.79	Corsair, near corrosion	7.6
DB58	DB58	Biofilm	15.20	Corsair, near non-corr.	7.6
DB59	DB60	Biofilm	11.90	P47, near corrosion	3.7
DB60	DB61	Biofilm	8.15	P47, near non-corr.	4.3
DB61	DB62	Biofilm	7.73	P47, near non-corr.	3.4
DB62	DB63	Biofilm	8.53	P47, near corrosion	3.0
DB63	DB64	Biofilm	6.07	P47, near non-corr.	3.0
DB64	DB65	Biofilm	5.63	P47, near non-corr.	3.0
DB65	DB66	Biofilm	7.20	P47, near corrosion	3.0
DB66	DB67	Biofilm	10.90	P47, near non-corr.	4.3
DB67	DB68	Biofilm	5.90	P47, near corrosion	4.3
DB68	DB69	Biofilm	8.68	P47, near non-corr.	3.7
DB69	DB70	Biofilm	8.43	P47, near corrosion	3.7
DB70	S2a	Sediment	1.45	Corsair, 30m away	7.9
DB71	S3a	Sediment	2.63	Corsair, near corrosion	7.9
DB72	S4a	Sediment	1.54	Corsair, 5m away	7.9
DB73	S5a	Sediment	1.38	Corsair, near non-corr.	7.9
DB74	S6a	Sediment	2.2	P47, 5m away	4.6
DB75	S7a	Sediment	1.5	P47, 30m away	4.6
DB76	S9a	Sediment	1.35	P47, near non-corr.	4.6
DB77	S10a	Sediment	2.3	P47, near corrosion	4.6
DB78	A	Water Filter	2.49	Corsair (840mL)	1
DB79	B	Water Filter	3	Corsair (780mL)	1
DB80	C	Water Filter	3.47	Corsair (840mL)	1
DB81	D	Water Filter	2.75	P47 (600mL)	1
DB82	E	Water Filter	2.19	P47 (600mL)	1
DB83	F	Water Filter	4.02	P47 (550mL)	1

Appendix B: Bacterial Taxonomic Data (Class Level)

Sequence totals at the class level are provided for each sample. Samples are ordered by site and type. Taxa are listed in alphabetical order, first by phylum and then by class. Cyanobacteria sequences identified as chloroplasts have been removed.

Hellcat: Corroded

Phylum	Class	DB02	DB05	DB07	DB08	DB84
Acidobacteria	Acidobacteria, Gp1-9	89	314	377	171	717
	Blastocatellia	6	23	15	1	37
	Holophagae	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0
	Unclassified	21	86	70	21	195
Actinobacteria	Acidimicrobiia	48	429	145	32	601
	Actinobacteria	5	34	11	4	47
	Rubrobacteria	0	0	0	0	0
	Thermoleophilia	2	7	9	5	21
	Unclassified	7	78	55	18	127
Aminicenantes	Saccharicenantaceae	1	4	0	0	3
	Unclassified	0	0	1	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0	2
	Armatimonadia	0	0	0	0	0
Bacteria	Unclassified	481	2001	949	610	2183
Bacteroidetes	Bacteroidia	7	15	15	4	8
	Chitinophagia	0	27	0	0	2
	Cytophagia	154	680	293	183	631
	Flavobacteriia	488	2415	956	527	1823
	Saprospiria	187	318	322	140	154
	Sphingobacteriia	0	0	0	0	0
	Unclassified	198	641	367	253	415
Balneolaeota	Balneolia	1	11	0	8	5
BRC1	Unclassified	0	0	0	0	0
Campilobacterota	Campylobacteria	0	0	0	0	0
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	0	1	1	0
Chlamydiae	Chlamydiia	0	0	0	0	1
Chloroflexi	Anaerolineae	7	23	20	8	25
	Caldilineae	1	12	4	1	9
	Dehalococcoidia	0	0	0	0	0
	Ktedonobacteria	0	1	0	0	0
	Thermomicrobia	0	3	1	1	0
	Unclassified	0	3	12	2	13

Cyanobacteria	Cyanobacteria	281	1080	391	134	874
Deferribacteres	Deferribacteres	1	3	3	2	1
Deinococcus- Thermus	Deinococci	4	26	13	2	10
Elusimicrobia	Endomicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	1	0	0
Firmicutes	Bacilli	13	75	51	13	275
	Clostridia	104	994	551	158	1767
	Erysipelotrichia	8	24	11	2	25
	Negativicutes	0	1	0	0	0
	Unclassified	9	60	52	17	119
Fusobacteria	Fusobacteriia	2	6	2	1	9
Gemmatimonadetes	Gemmatimonadetes	0	1	1	0	2
Hydrogenedentes	Candidatus Hygrodenedens	1	2	6	1	4
Ignavibacteriae	Ignavibacteria	3	3	29	11	9
Kiritimatiellaeota	Kiritimatiellae	0	3	1	5	4
Latescibacteria	Unclassified	0	1	9	2	5
Lentisphaerae	Lentisphaeria	0	2	0	4	0
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	0	0	0	1	0
Parcubacteria	Unclassified	0	0	0	0	0
Planctomycetes	Phycisphaerae	41	208	98	23	137
	Planctomycetacia	1080	7100	3881	1147	11922
	Unclassified	11	49	14	13	43
Poribacteria	Unclassified	1	1	0	0	0
Proteobacteria	Alphaproteobacteria	990	6778	2429	1179	11952
	Betaproteobacteria	0	5	0	2	8
	Deltaproteobacteria	125	447	555	256	651
	Gammaproteobacteria	793	4068	1629	1167	4257
	Oligoflexia	13	114	33	18	94
	Unclassified	68	527	166	109	641
	Zetaproteobacteria	0	0	0	0	0
Rhodothermaeota	Rhodothermia	26	101	87	41	42
Spirochaetes	Spirochaetia	1	5	14	7	3
SR1	Unclassified	0	0	0	0	1
Verrucomicrobia	Opitutae	7	17	2	8	11
	Spartobacteria	0	0	0	0	1
	Subdivision3	4	14	1	6	4
	Subdivision5	0	0	2	1	0
	Unclassified	9	36	14	5	38
	Verrucomicrobiae	55	254	146	37	391

Hellcat: Non-Corroded

Phylum	Class	DB01	DB03	DB04	DB09	DB10
Acidobacteria	Acidobacteria, Gp1-9	70	118	78	160	226
	Blastocatellia	1	2	0	7	4
	Holophagae	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0
	Unclassified	11	31	20	32	44
Actinobacteria	Acidimicrobiia	97	95	46	79	214
	Actinobacteria	9	7	2	7	17
	Rubrobacteria	0	0	0	0	0
	Thermoleophilia	1	3	1	6	8
	Unclassified	21	28	9	21	60
Aminicenantes	Saccharicenantaceae	1	4	0	2	0
	Unclassified	0	0	0	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0	2
	Armatimonadia	0	0	0	0	0
Bacteria	Unclassified	581	604	370	681	760
Bacteroidetes	Bacteroidia	7	12	11	22	3
	Chitinophagia	2	0	1	0	3
	Cytophagia	348	146	143	122	171
	Flavobacteriia	1886	2062	451	507	740
	Saprospiria	323	221	118	175	124
	Sphingobacteriia	0	0	0	0	0
	Unclassified	324	321	188	197	155
Balneolaeota	Balneolia	1	1	3	0	1
BRC1	Unclassified	0	0	0	0	1
Campilobacterota	Campylobacteria	0	1	0	1	0
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	0	1	0	1
Chlamydiae	Chlamydiia	0	0	1	0	0
Chloroflexi	Anaerolineae	5	11	3	9	42
	Caldilineae	5	3	0	5	2
	Dehalococcoidia	0	0	0	0	0
	Ktedonobacteria	0	1	0	0	0
	Thermomicrobia	0	1	0	0	0
	Unclassified	6	10	3	4	5
Cyanobacteria	Cyanobacteria	827	1246	169	167	407
Deferribacteres	Deferribacteres	1	5	7	3	1
Deinococcus- Thermus	Deinococci	13	12	4	5	20
Elusimicrobia	Endomicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0
Firmicutes	Bacilli	35	38	17	24	52
	Clostridia	451	377	168	197	318
	Erysipelotrichia	6	5	5	2	7
	Negativicutes	0	1	0	0	2

	Unclassified	31	30	20	20	31
Fusobacteria	Fusobacteriia	3	4	10	4	1
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	1	0	0	1	2
Ignavibacteriae	Ignavibacteria	1	4	5	21	2
Kiritimatiellaeota	Kiritimatiellae	0	0	1	2	0
Latescibacteria	Unclassified	0	4	1	3	0
Lentisphaerae	Lentisphaeria	0	0	0	0	0
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	0	0	1	1	0
Parcubacteria	Unclassified	0	0	0	0	0
Planctomycetes	Phycisphaerae	132	139	89	35	71
	Planctomycetacia	2204	3340	924	1445	3213
	Unclassified	15	5	9	12	3
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	3181	4533	970	1536	2913
	Betaproteobacteria	0	1	1	1	3
	Deltaproteobacteria	140	200	133	444	290
	Gammaproteobacteria	754	785	690	907	1286
	Oligoflexia	45	37	12	23	24
	Unclassified	154	186	75	107	213
	Zetaproteobacteria	0	0	0	0	0
Rhodothermaeota	Rhodothermia	21	29	16	29	55
Spirochaetes	Spirochaetia	2	6	9	15	6
SR1	Unclassified	0	1	0	0	0
Verrucomicrobia	Opitutae	0	3	4	3	1
	Spartobacteria	0	0	0	0	0
	Subdivision3	2	1	0	0	1
	Subdivision5	0	0	0	0	0
	Unclassified	9	9	4	7	28
	Verrucomicrobiae	175	91	52	58	129

Hellcat: Steel (DB12), Tire (DB85), and Sponge-Collected Samples (DB39-40)

Phylum	Class	DB12	DB85	DB39	DB40
Acidobacteria	Acidobacteria, Gp1-9	82	326	92	105
	Blastocatellia	0	12	5	7
	Holophagae	0	0	1	0
	Thermoanaerobaculia	0	0	0	0
	Unclassified	11	51	23	31
Actinobacteria	Acidimicrobiia	17	35	70	71
	Actinobacteria	3	34	3	5
	Rubrobacteria	0	0	0	0
	Thermoleophilia	2	4	0	1
	Unclassified	9	27	9	13
Aminicenantes	Saccharicenantaceae	0	0	0	2
	Unclassified	0	0	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0
	Armatimonadia	0	0	0	0
Bacteria	Unclassified	1320	758	430	575
Bacteroidetes	Bacteroidia	6	62	7	7
	Chitinophagia	0	1	0	3
	Cytophagia	71	48	152	171
	Flavobacteriia	194	200	488	704
	Saprospiria	63	71	230	255
	Sphingobacteriia	0	1	0	0
	Unclassified	143	106	215	265
Balneolaeota	Balneolia	4	0	4	2
BRC1	Unclassified	1	0	0	0
Campilobacterota	Campylobacteria	0	1	0	0
Candidate division WPS-1	Unclassified	0	6	0	0
Candidate division ZB3	Unclassified	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	1	0	0
Chlamydiae	Chlamydiia	0	0	0	0
Chloroflexi	Anaerolineae	11	14	2	6
	Caldilineae	1	0	2	6
	Dehalococcoidia	0	0	0	0
	Ktedonobacteria	0	0	0	0
	Thermomicrobia	1	1	1	0
	Unclassified	5	10	2	2
Cyanobacteria	Cyanobacteria	135	31	235	302
Deferribacteres	Deferribacteres	3	8	0	1
Deinococcus- Thermus	Deinococci	1	5	2	5
Elusimicrobia	Endomicrobia	0	0	0	0
Fibrobacteres	Chitinispirillia	1	0	0	0
Firmicutes	Bacilli	0	41	13	15
	Clostridia	50	77	152	187
	Erysipelotrichia	0	6	6	1
	Negativicutes	0	3	0	1

	Unclassified	8	6	16	23
Fusobacteria	Fusobacteriia	4	8	7	16
Gemmatimonadetes	Gemmatimonadetes	0	3	0	0
Hydrogenedentes	Candidatus Hygrodenedens	0	3	0	1
Ignavibacteriae	Ignavibacteria	3	13	2	1
Kiritimatiellaeota	Kiritimatiellae	3	16	1	4
Latescibacteria	Unclassified	4	6	0	0
Lentisphaerae	Lentisphaeria	1	0	2	2
Marinimicrobia	Unclassified	0	0	0	2
Microgenomates	Unclassified	0	0	0	0
Nitrospirae	Nitrospira	7	0	0	0
Parcubacteria	Unclassified	0	0	0	0
Planctomycetes	Phycisphaerae	12	10	36	41
	Planctomycetacia	223	486	941	1097
	Unclassified	22	3	12	12
Poribacteria	Unclassified	0	0	0	0
Proteobacteria	Alphaproteobacteria	480	685	1414	1775
	Betaproteobacteria	1	30	2	0
	Deltaproteobacteria	290	195	183	237
	Gammaproteobacteria	591	620	976	1219
	Oligoflexia	6	60	18	32
	Unclassified	302	139	72	130
	Zetaproteobacteria	0	0	0	0
Rhodothermaeota	Rhodothermia	5	13	15	20
Spirochaetes	Spirochaetia	8	31	3	12
SR1	Unclassified	0	0	0	0
Verrucomicrobia	Opitutae	3	0	1	6
	Spartobacteria	0	2	0	0
	Subdivision3	1	2	1	4
	Subdivision5	0	0	0	0
	Unclassified	2	4	3	5
	Verrucomicrobiae	8	46	46	61

Helldiver: Corroded

Phylum	Class	DB16	DB18	DB19	DB20	DB22
Acidobacteria	Acidobacteria, Gp1-9	80	21	82	94	53
	Blastocatellia	1	0	4	2	1
	Holophagae	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0
	Unclassified	5	2	10	21	39
Actinobacteria	Acidimicrobiia	35	22	63	107	72
	Actinobacteria	2	1	5	6	0
	Rubrobacteria	0	0	0	0	0
	Thermoleophilia	1	0	2	0	2
	Unclassified	12	4	10	19	33
Aminicenantes	Saccharicenantaceae	0	0	0	1	1
	Unclassified	0	0	1	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0	0
	Armatimonadia	0	0	0	0	0
Bacteria	Unclassified	786	511	467	916	1084
Bacteroidetes	Bacteroidia	6	0	3	2	13
	Chitinophagia	0	1	3	4	1
	Cytophagia	201	184	500	448	381
	Flavobacteriia	2009	1166	792	1369	3178
	Saprospiria	145	97	36	39	263
	Sphingobacteriia	0	0	0	0	0
	Unclassified	154	143	110	158	453
Balneolaeota	Balneolia	2	2	1	0	8
BRC1	Unclassified	0	0	0	0	0
Campilobacterota	Campylobacteria	0	0	0	0	1
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	0	0	0	0
Chlamydiae	Chlamydiia	1	0	0	0	0
Chloroflexi	Anaerolineae	15	0	6	1	15
	Caldilineae	2	2	8	6	1
	Dehalococcoidia	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0
	Thermomicrobia	0	0	0	0	0
	Unclassified	1	0	2	4	8
Cyanobacteria	Cyanobacteria	3836	1332	413	691	3740
Deferribacteres	Deferribacteres	4	0	1	0	3
Deinococcus- Thermus	Deinococci	4	6	0	1	6
Elusimicrobia	Endomicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0
Firmicutes	Bacilli	14	0	5	20	4
	Clostridia	356	20	226	236	112
	Erysipelotrichia	4	0	10	12	3
	Negativicutes	0	0	1	0	0

	Unclassified	17	2	6	30	16
Fusobacteria	Fusobacteriia	7	0	1	4	11
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	3	0	2	0	0
Ignavibacteriae	Ignavibacteria	2	0	2	0	1
Kiritimatiellaeota	Kiritimatiellae	1	0	0	0	2
Latescibacteria	Unclassified	0	0	0	0	0
Lentisphaerae	Lentisphaeria	1	0	1	0	2
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	0	0	0	0	0
Parcubacteria	Unclassified	0	0	0	0	0
Planctomycetes	Phycisphaerae	269	247	185	226	642
	Planctomycetacia	1929	1000	3493	4568	2499
	Unclassified	23	28	18	34	8
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	4626	2381	2747	5328	6191
	Betaproteobacteria	1	1	0	0	1
	Deltaproteobacteria	139	31	103	243	251
	Gammaproteobacteria	975	526	1654	2328	2178
	Oligoflexia	82	20	37	40	103
	Unclassified	204	113	153	257	338
	Zetaproteobacteria	0	0	0	0	1
Rhodothermaeota	Rhodothermia	15	26	8	7	36
Spirochaetes	Spirochaetia	1	3	1	0	3
SR1	Unclassified	0	0	0	0	0
Verrucomicrobia	Opitutae	6	5	0	3	12
	Spartobacteria	0	0	0	0	0
	Subdivision3	1	0	0	4	0
	Subdivision5	0	0	0	0	0
	Unclassified	5	2	9	23	35
	Verrucomicrobiae	53	21	92	182	82

Helldiver: Non-Corroded

Phylum	Class	DB13	DB14	DB15	DB17	DB21
Acidobacteria	Acidobacteria, Gp1-9	68	339	48	30	85
	Blastocatellia	3	3	1	1	0
	Holophagae	0	1	0	0	0
	Thermoanaerobaculia	0	0	0	0	0
	Unclassified	56	59	7	8	72
Actinobacteria	Acidimicrobiia	156	221	89	177	129
	Actinobacteria	8	7	6	11	4
	Rubrobacteria	0	0	0	0	0
	Thermoleophilia	0	3	0	0	1
	Unclassified	65	59	12	11	35
Aminicenantes	Saccharicenantaceae	0	4	1	0	2
	Unclassified	0	0	0	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0	0
	Armatimonadia	0	0	0	0	0
Bacteria	Unclassified	1182	2350	836	454	1775
Bacteroidetes	Bacteroidia	6	15	0	0	6
	Chitinophagia	1	1	15	4	12
	Cytophagia	222	709	143	353	298
	Flavobacteriia	3143	2300	1326	892	4640
	Saprospiria	141	451	45	23	582
	Sphingobacteriia	0	0	0	0	0
	Unclassified	226	761	174	112	565
Balneolaeota	Balneolia	3	65	3	0	0
BRC1	Unclassified	0	0	0	0	0
Campilobacterota	Campylobacteria	0	2	0	0	0
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	0	0	0	1
Chlamydiae	Chlamydiia	0	4	0	1	0
Chloroflexi	Anaerolineae	8	38	53	20	15
	Caldilineae	3	7	2	1	11
	Dehalococcoidia	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0
	Thermomicrobia	0	2	0	0	0
	Unclassified	8	12	0	0	28
Cyanobacteria	Cyanobacteria	8863	887	1656	1283	9982
Deferribacteres	Deferribacteres	1	16	2	0	5
Deinococcus- Thermus	Deinococci	32	19	8	1	21
Elusimicrobia	Endomicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0
Firmicutes	Bacilli	16	42	7	12	7
	Clostridia	384	444	139	422	118
	Erysipelotrichia	42	9	3	16	7
	Negativicutes	0	0	0	0	0

	Unclassified	38	61	9	24	14
Fusobacteria	Fusobacteriia	3	23	2	0	2
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	0	5	1	0	2
Ignavibacteriae	Ignavibacteria	1	9	1	1	2
Kiritimatiellaeota	Kiritimatiellae	2	8	0	0	0
Latescibacteria	Unclassified	1	4	1	0	2
Lentisphaerae	Lentisphaeria	0	12	1	0	0
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	0	2	0	0	0
Parcubacteria	Unclassified	0	0	0	0	0
Planctomycetes	Phycisphaerae	889	77	446	268	808
	Planctomycetacia	5855	2150	2863	4193	4797
	Unclassified	22	49	96	29	39
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	11047	4203	3997	4038	9361
	Betaproteobacteria	0	9	2	0	2
	Deltaproteobacteria	171	604	127	77	302
	Gammaproteobacteria	1514	4141	1726	1114	1948
	Oligoflexia	93	133	59	56	153
	Unclassified	345	446	231	193	523
	Zetaproteobacteria	0	0	0	0	0
Rhodothermaeota	Rhodothermia	117	100	55	3	65
Spirochaetes	Spirochaetia	3	15	1	0	3
SR1	Unclassified	1	0	0	0	0
Verrucomicrobia	Opitutae	14	24	4	7	5
	Spartobacteria	0	0	0	0	0
	Subdivision3	0	2	1	0	1
	Subdivision5	0	1	0	0	0
	Unclassified	18	5	12	14	13
	Verrucomicrobiae	144	93	99	141	98

Hellcat: Sediment

Phylum	Class	DB23	DB24	DB26	DB86	DB87
Acidobacteria	Acidobacteria, Gp1-9	512	446	518	8167	7044
	Blastocatellia	0	4	1	23	39
	Holophagae	0	0	0	5	2
	Thermoanaerobaculia	7	0	0	2	2
	Unclassified	59	62	61	1346	765
Actinobacteria	Acidimicrobiia	28	32	20	619	353
	Actinobacteria	25	3	5	37	70
	Rubrobacteria	0	0	0	0	1
	Thermoleophilia	15	3	1	29	22
	Unclassified	31	22	15	363	294
Aminicenantes	Saccharicenantaceae	15	16	13	138	292
	Unclassified	3	0	0	20	39
Armatimonadetes	Armatimonadetes	1	0	0	2	1
	Armatimonadia	0	0	0	0	0
Bacteria	Unclassified	1307	987	1072	20947	15519
Bacteroidetes	Bacteroidia	84	12	44	496	679
	Chitinophagia	0	1	0	1	5
	Cytophagia	83	64	59	2068	1082
	Flavobacteriia	133	269	119	3160	2603
	Saprospiria	27	65	44	1873	942
	Sphingobacteriia	0	0	0	0	0
	Unclassified	119	87	86	2564	1714
Balneolaeota	Balneolia	0	1	0	8	8
BRC1	Unclassified	2	0	2	3	4
Campilobacterota	Campylobacteria	12	0	0	12	0
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	1	3
Candidatus Saccharibacteria	Unclassified	1	0	1	10	4
Chlamydiae	Chlamydiia	0	0	0	0	1
Chloroflexi	Anaerolineae	60	24	50	836	640
	Caldilineae	4	8	4	60	63
	Dehalococcoidia	0	0	0	0	2
	Ktedonobacteria	0	0	0	1	0
	Thermomicrobia	0	0	0	2	4
	Unclassified	40	29	41	407	407
Cyanobacteria	Cyanobacteria	7	21	11	140	266
Deferribacteres	Deferribacteres	41	38	45	639	635
Deinococcus- Thermus	Deinococci	1	4	4	90	33
Elusimicrobia	Endomicrobia	0	0	0	1	2
Fibrobacteres	Chitinispirillia	4	0	0	4	13
Firmicutes	Bacilli	105	33	26	222	283
	Clostridia	430	65	94	2209	1132
	Erysipelotrichia	6	0	1	56	11
	Negativicutes	0	1	0	4	5

	Unclassified	116	39	39	259	376
Fusobacteria	Fusobacteriia	3	2	4	58	41
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	11	2	4	74	22
Ignavibacteriae	Ignavibacteria	23	42	32	541	704
Kiritimatiellaeota	Kiritimatiellae	9	3	7	67	92
Latescibacteria	Unclassified	12	21	21	209	237
Lentisphaerae	Lentisphaeria	0	0	0	7	1
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	1	0	0	166	1
Parcubacteria	Unclassified	0	0	1	0	0
Planctomycetes	Phycisphaerae	29	18	22	384	322
	Planctomycetacia	791	570	573	18505	10834
	Unclassified	22	8	13	533	269
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	652	513	333	10648	6723
	Betaproteobacteria	0	0	0	33	18
	Deltaproteobacteria	904	637	715	8420	9455
	Gammaproteobacteria	775	911	841	26730	13313
	Oligoflexia	17	9	3	214	100
	Unclassified	118	96	109	2315	1322
	Zetaproteobacteria	1	0	0	0	0
Rhodothermaeota	Rhodothermia	22	22	18	546	320
Spirochaetes	Spirochaetia	89	32	63	1024	856
SR1	Unclassified	0	0	0	0	0
Verrucomicrobia	Opitutae	1	2	2	67	70
	Spartobacteria	0	0	0	0	1
	Subdivision3	3	5	3	19	42
	Subdivision5	3	0	1	11	15
	Unclassified	3	2	3	42	42
	Verrucomicrobiae	6	13	7	313	162

Helldiver: Sediment

Phylum	Class	DB29	DB30	DB31	DB88	DB89
Acidobacteria	Acidobacteria, Gp1-9	1086	320	775	509	972
	Blastocatellia	0	0	2	0	2
	Holophagae	0	0	0	0	0
	Thermoanaerobaculia	2	1	0	0	0
	Unclassified	87	64	113	91	96
Actinobacteria	Acidimicrobiia	53	43	35	25	21
	Actinobacteria	27	4	1	11	11
	Rubrobacteria	0	0	0	0	0
	Thermoleophilia	5	6	0	1	2
	Unclassified	44	40	45	18	39
Aminicenantes	Saccharicenantaceae	15	21	23	8	30
	Unclassified	1	5	2	0	0
Armatimonadetes	Armatimonadetes	1	0	0	0	0
	Armatimonadia	0	0	0	0	8
Bacteria	Unclassified	2030	915	2112	956	1674
Bacteroidetes	Bacteroidia	116	17	37	43	25
	Chitinophagia	0	0	0	1	9
	Cytophagia	257	98	137	103	92
	Flavobacteriia	274	121	334	156	203
	Saprospiria	66	37	135	69	35
	Sphingobacteriia	0	0	0	0	0
	Unclassified	243	87	199	82	104
Balneolaeota	Balneolia	0	0	3	0	0
BRC1	Unclassified	0	1	1	0	0
Campilobacterota	Campylobacteria	4	9	0	0	0
Candidate division WPS-1	Unclassified	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	1	0	0	1	2
Chlamydiae	Chlamydiia	0	1	0	0	0
Chloroflexi	Anaerolineae	96	50	91	28	53
	Caldilineae	12	3	7	1	1
	Dehalococcoidia	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0
	Thermomicrobia	0	0	0	0	0
	Unclassified	77	18	61	17	47
Cyanobacteria	Cyanobacteria	9	5	17	16	34
Deferribacteres	Deferribacteres	89	12	114	43	81
Deinococcus- Thermus	Deinococci	3	3	5	0	6
Elusimicrobia	Endomicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	3	0	0	0	1
Firmicutes	Bacilli	107	30	16	20	27
	Clostridia	705	281	111	101	106
	Erysipelotrichia	17	6	1	3	0
	Negativicutes	1	1	0	0	0

	Unclassified	201	38	44	44	79
Fusobacteria	Fusobacteriia	1	11	0	3	0
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	11	4	6	5	1
Ignavibacteriae	Ignavibacteria	30	6	129	48	85
Kiritimatiellaeota	Kiritimatiellae	5	1	5	2	10
Latescibacteria	Unclassified	26	4	39	13	19
Lentisphaerae	Lentisphaeria	0	0	0	2	0
Marinimicrobia	Unclassified	0	0	0	0	0
Microgenomates	Unclassified	0	0	1	0	0
Nitrospirae	Nitrospira	3	8	0	0	0
Parcubacteria	Unclassified	0	0	0	0	0
Planctomycetes	Phycisphaerae	49	23	48	12	26
	Planctomycetacia	1930	886	1154	650	892
	Unclassified	30	19	47	11	23
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	1373	628	947	449	882
	Betaproteobacteria	2	2	0	36	59
	Deltaproteobacteria	1782	433	1352	520	1064
	Gammaproteobacteria	1784	1056	2197	1030	1794
	Oligoflexia	22	4	35	13	2
	Unclassified	264	139	193	83	193
	Zetaproteobacteria	0	0	1	0	0
Rhodothermaeota	Rhodothermia	44	14	52	21	18
Spirochaetes	Spirochaetia	131	22	88	88	148
SR1	Unclassified	0	0	0	0	0
Verrucomicrobia	Opitutae	7	3	5	1	4
	Spartobacteria	0	0	0	0	0
	Subdivision3	0	1	3	2	1
	Subdivision5	2	0	2	3	0
	Unclassified	3	2	3	0	0
	Verrucomicrobiae	16	14	23	10	4

Seawater: Hellcat (DB33, DB34, DB37) and Helldiver (DB35, DB36, DB38)

Phylum	Class	DB33	DB34	DB35	DB37	DB36	DB38
Acidobacteria	Acidobacteria, Gp1-9	12	1	0	21	1	1
	Blastocatellia	0	0	0	0	0	0
	Holophagae	0	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0	0
	Unclassified	1	1	0	2	0	0
Actinobacteria	Acidimicrobiia	0	0	0	1	0	8
	Actinobacteria	0	0	0	0	0	0
	Rubrobacteria	0	0	0	0	0	0
	Thermoleophilia	0	0	0	0	0	0
	Unclassified	3	1	1	0	1	4
Aminicenantes	Saccharicenantaceae	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Armatimonadetes	Armatimonadetes	0	0	0	0	0	0
	Armatimonadia	0	0	0	0	0	0
Bacteria	Unclassified	221	259	112	286	461	578
Bacteroidetes	Bacteroidia	15	0	8	12	0	1
	Chitinophagia	0	0	0	1	0	0
	Cytophagia	19	38	22	44	84	82
	Flavobacteriia	6398	1851	3335	6726	2598	3980
	Saprospiria	30	17	14	33	11	17
	Sphingobacteriia	0	0	0	0	0	0
	Unclassified	190	68	122	296	90	144
Balneolaeota	Balneolia	1	0	0	0	1	1
BRC1	Unclassified	0	0	0	0	0	0
Campilobacterota	Campylobacteria	1	0	0	1	0	0
Candidate division WPS-1	Unclassified	0	0	0	0	0	0
Candidate division ZB3	Unclassified	0	0	0	1	0	0
Candidatus Saccharibacteria	Unclassified	0	0	0	0	0	0
Chlamydiae	Chlamydiia	0	0	0	0	0	0
Chloroflexi	Anaerolineae	0	0	0	0	0	0
	Caldilineae	0	0	0	0	0	0
	Dehalococcoidia	0	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0	0
	Thermomicrobia	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Cyanobacteria	Cyanobacteria	1151	3866	466	1159	4612	8409
Deferribacteres	Deferribacteres	0	0	0	1	0	0
Deinococcus-Thermus	Deinococci	0	0	0	2	0	0
Elusimicrobia	Endomicrobia	0	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0	0
Firmicutes	Bacilli	0	0	0	2	0	0
	Clostridia	5	0	4	13	0	1
	Erysipelotrichia	2	0	0	1	0	0

	Negativicutes	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Fusobacteria	Fusobacteriia	7	0	2	9	1	0
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0	0
Hydrogenedentes	Candidatus Hygrodenedens	0	0	0	0	0	0
Ignavibacteriae	Ignavibacteria	2	0	0	1	0	0
Kiritimatiellaeota	Kiritimatiellae	1	0	2	2	0	0
Latescibacteria	Unclassified	0	0	0	0	0	0
Lentisphaerae	Lentisphaeria	1	0	0	4	2	0
Marinimicrobia	Unclassified	2	20	7	4	11	27
Microgenomates	Unclassified	0	0	0	0	0	0
Nitrospirae	Nitrospira	1	0	0	1	0	0
Parcubacteria	Unclassified	0	0	0	0	0	1
Planctomycetes	Phycisphaerae	6	0	1	8	1	0
	Planctomycetacia	53	4	18	73	8	10
	Unclassified	2	20	1	6	20	33
Poribacteria	Unclassified	0	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	3909	1426	1740	3428	2272	3420
	Betaproteobacteria	5	12	2	7	9	19
	Deltaproteobacteria	31	2	8	29	3	7
	Gammaproteobacteria	358	317	176	471	362	629
	Oligoflexia	6	0	12	27	3	1
	Unclassified	52	114	24	73	145	237
	Zetaproteobacteria	0	0	0	0	0	0
Rhodothermaeota	Rhodothermia	2	1	2	2	0	1
Spirochaetes	Spirochaetia	2	0	0	3	0	0
SR1	Unclassified	0	0	0	0	0	0
Verrucomicrobia	Opitutae	2	2	2	5	2	8
	Spartobacteria	0	0	0	0	0	0
	Subdivision3	0	0	0	0	0	0
	Subdivision5	0	0	0	0	0	0
	Unclassified	1	0	1	2	0	0
	Verrucomicrobiae	14	0	5	18	0	0

Corsair: Corroded

Phylum	Class	DB51	DB52	DB53	DB57
Abditibacteriota	Abditibacteria	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	1532	1147	546	2048
	Blastocatellia	49	46	16	66
	Holophagae	0	0	0	0
	Thermoanaerobaculia	0	0	0	0
	Unclassified	159	104	62	238
Actinobacteria	Acidimicrobiia	335	490	358	1610
	Actinobacteria	25	66	38	128
	Coriobacteriia	0	0	0	0
	Nitriliruptoria	0	0	0	0
	Thermoleophilia	11	8	3	13
	Unclassified	157	128	109	390
Aminicenantes	Saccharicenantaceae	0	0	0	0
	Unclassified	0	0	0	0
Armatimonadetes	Armatimonadia	0	0	0	0
	Unclassified	0	0	0	0
Bacteroidetes	Bacteroidia	61	24	9	221
	Chitinophagia	9	23	9	31
	Cytophagia	803	1137	781	2802
	Flavobacteriia	2231	2839	2261	7533
	Saprospiria	474	378	264	1107
	Sphingobacteriia	0	0	0	0
	Unclassified	1827	2718	1457	4367
Bacteria	Unclassified	5698	5542	3632	15944
Balneolaeota	Balneolia	8	10	11	16
Campilobacterota	Campylobacteria	0	0	0	1
Candidate Division WPS-1	Unclassified	0	0	0	0
Candidatus Saccharibacteria	Unclassified	1	0	0	2
Chlamydiae	Chlamydiia	1	0	0	12
Chloroflexi	Anaerolineae	19	36	11	98
	Caldilineae	23	28	27	107
	Chloroflexia	0	0	0	0
	Ktedonobacteria	0	0	0	0
	Thermomicrobia	1	4	0	14
	Unclassified	18	5	14	32
Cyanobacteria	Cyanobacteria	1199	1773	2315	5387
Deferribacteres	Deferribacteres	8	6	5	15
Deinococcus- Thermus	Deinococci	59	184	86	113
Elusimicrobia	Elusimicrobia	0	0	0	0
Fibrobacteres	Chitinispirillia	1	3	0	0
Firmicutes	Bacilli	34	38	23	46
	Clostridia	814	1234	592	1748
	Erysipelotrichia	22	42	34	33
	Negativicutes	0	0	4	1

	Unclassified	20	27	10	61
Fusobacteria	Fusobacteriia	1	4	7	13
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0
	Longimicrobia	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	9	5	2	7
Ignavibacteriae	Ignavibacteria	29	23	3	84
Kiritimatiellaeota	Kiritimatiellae	20	2	8	31
Latescibacteria	Unclassified	6	5	0	16
Lentisphaerae	Lentisphaeria	1	1	0	1
	Unclassified	0	2	1	0
Marinimicrobia	Unclassified	0	0	0	0
Nitrospirae	Nitrospira	11	3	0	2
Parcubacteria	Parcubacteria	0	0	0	2
Planctomycetes	Phycisphaerae	206	248	251	991
	Planctomycetacia	15088	15230	10460	34631
	Unclassified	212	171	109	647
Poribacteria	Unclassified	1	2	1	72
Proteobacteria	Alphaproteobacteria	9318	12377	10190	28746
	Betaproteobacteria	19	26	3	16
	Deltaproteobacteria	2190	1571	1009	4922
	Gammaproteobacteria	6826	6042	4555	14985
	Hydrogenophilalia	0	0	0	0
	Oligoflexia	52	93	57	186
	Unclassified	722	742	510	1778
Rhodothermaeota	Rhodothermia	131	93	105	718
Spirochaetes	Spirochaetia	81	31	27	189
SR1	Unclassified	0	0	0	0
Synergistetes	Synergistia	0	0	0	0
Verrucomicrobia	Opitutae	10	23	25	76
	Spartobacteria	0	0	0	0
	Subdivision3	8	11	8	28
	Subdivision5	0	0	0	1
	Terrimicrobia	0	0	0	0
	Unclassified	67	113	45	162
	Verrucomicrobiae	154	244	98	503

Corsair: Non-Corroded

Phylum	Class	DB54	DB55	DB56	DB58
Abditibacteriota	Abditibacteria	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	849	273	512	4036
	Blastocatellia	16	4	13	86
	Holophagae	0	0	0	0
	Thermoanaerobaculia	0	0	0	0
	Unclassified	120	66	35	330
Actinobacteria	Acidimicrobiia	698	493	58	1378
	Actinobacteria	0	22	4	237
	Coriobacteriia	0	0	0	0
	Nitriliruptoria	0	0	0	0
	Thermoleophilia	2	1	2	36
	Unclassified	126	95	43	486
Aminicenantes	Saccharicenantaceae	0	0	1	0
	Unclassified	0	0	0	0
Armatimonadetes	Armatimonadia	0	0	0	0
	Unclassified	0	0	0	0
Bacteroidetes	Bacteroidia	31	17	5	63
	Chitinophagia	7	7	1	44
	Cytophagia	2217	727	117	2583
	Flavobacteriia	5184	6311	364	6329
	Saprospiria	594	397	120	741
	Sphingobacteriia	1	0	3	0
	Unclassified	2911	2209	359	3215
Bacteria	Unclassified	3362	3398	1443	12249
Balneolaeota	Balneolia	23	8	0	1
Campilobacterota	Campylobacteria	0	0	1	1
Candidate Division WPS-1	Unclassified	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	0	0	3
Chlamydiae	Chlamydiia	0	2	1	9
Chloroflexi	Anaerolineae	20	389	20	134
	Caldilineae	29	10	5	63
	Chloroflexia	0	0	0	0
	Ktedonobacteria	0	0	0	0
	Thermomicrobia	0	0	8	18
	Unclassified	8	10	9	32
Cyanobacteria	Cyanobacteria	4484	8365	154	3342
Deferribacteres	Deferribacteres	3	2	4	16
Deinococcus- Thermus	Deinococci	52	16	10	87
Elusimicrobia	Elusimicrobia	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	2	0
Firmicutes	Bacilli	24	19	2	88
	Clostridia	1406	419	122	2582
	Erysipelotrichia	93	19	7	76
	Negativicutes	0	0	0	0

	Unclassified	30	10	1	83
Fusobacteria	Fusobacteriia	17	8	1	21
Gemmatimonadetes	Gemmatimonadetes	0	0	0	2
	Longimicrobia	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	3	2	0	8
Ignavibacteriae	Ignavibacteria	2	3	0	91
Kiritimatiellaeota	Kiritimatiellae	2	4	2	13
Latescibacteria	Unclassified	1	0	2	7
Lentisphaerae	Lentisphaeria	2	0	1	5
	Unclassified	0	0	0	2
Marinimicrobia	Unclassified	0	0	0	0
Nitrospirae	Nitrospira	1	1	13	12
Parcubacteria	Parcubacteria	0	0	0	0
Planctomycetes	Phycisphaerae	413	1304	37	649
	Planctomycetacia	19034	13711	2215	41786
	Unclassified	164	250	39	380
Poribacteria	Unclassified	0	0	0	3
Proteobacteria	Alphaproteobacteria	16595	20763	1975	30601
	Betaproteobacteria	7	3	11	13
	Deltaproteobacteria	729	625	435	3308
	Gammaproteobacteria	9171	3468	1732	13089
	Hydrogenophilalia	0	0	0	0
	Oligoflexia	193	101	14	83
	Unclassified	957	617	178	1534
Rhodothermaeota	Rhodothermia	189	75	43	273
Spirochaetes	Spirochaetia	5	2	14	69
SR1	Unclassified	0	0	0	0
Synergistetes	Synergistia	0	0	0	0
Verrucomicrobia	Opitutae	27	16	6	19
	Spartobacteria	0	0	0	0
	Subdivision3	16	0	2	8
	Subdivision5	0	0	0	0
	Terrimicrobia	0	0	0	0
	Unclassified	63	38	20	267
	Verrucomicrobiae	354	199	27	550

Thunderbolt: Corroded

Phylum	Class	DB59	DB62	DB65	DB67	DB69
Abditibacteriota	Abditibacteria	0	1	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	467	132	389	703	225
	Blastocatellia	19	2	46	6	12
	Holophagae	0	0	1	10	0
	Thermoanaerobaculia	0	0	0	0	0
	Unclassified	56	22	63	50	39
Actinobacteria	Acidimicrobiia	1269	556	842	456	877
	Actinobacteria	12	2	1	6	2
	Coriobacteriia	0	0	0	0	0
	Nitriliruptoria	1	0	0	0	1
	Thermoleophilia	0	0	0	1	0
	Unclassified	115	55	110	147	70
Aminicenantes	Saccharicenantaceae	0	0	0	0	0
	Unclassified	0	0	0	0	0
Armatimonadetes	Armatimonadia	0	0	0	0	0
	Unclassified	0	0	6	0	3
Bacteroidetes	Bacteroidia	26	8	32	29	6
	Chitinophagia	10	15	44	25	26
	Cytophagia	3090	998	2098	2115	1562
	Flavobacteriia	13169	6018	9611	10583	5957
	Saprospiria	656	422	699	1771	453
	Sphingobacteriia	0	0	0	0	0
	Unclassified	2626	1810	2802	6829	1282
Bacteria	Unclassified	2931	2380	3826	4854	2289
Balneolaeota	Balneolia	9	4	8	3	2
Campilobacterota	Campylobacteria	0	0	0	0	0
Candidate Division WPS-1	Unclassified	15	0	3	5	11
Candidatus Saccharibacteria	Unclassified	0	0	0	1	0
Chlamydiae	Chlamydiia	2	0	2	0	3
Chloroflexi	Anaerolineae	71	51	56	112	82
	Caldilineae	23	45	23	78	19
	Chloroflexia	0	0	0	0	8
	Ktedonobacteria	0	0	0	0	0
	Thermomicrobia	0	0	0	0	1
	Unclassified	6	52	77	33	36
Cyanobacteria	Cyanobacteria	15800	2255	27721	9276	14221
Deferribacteres	Deferribacteres	1	0	0	1	0
Deinococcus- Thermus	Deinococci	836	341	602	1058	377
Elusimicrobia	Elusimicrobia	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0
Firmicutes	Bacilli	8	0	7	5	8
	Clostridia	698	175	700	412	433
	Erysipelotrichia	37	23	51	33	46
	Negativicutes	0	0	0	1	0

	Unclassified	31	5	13	7	19
Fusobacteria	Fusobacteriia	18	8	14	21	5
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0
	Longimicrobia	0	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	1	1	2	0	2
Ignavibacteriae	Ignavibacteria	1	4	2	0	0
Kiritimatiellaeota	Kiritimatiellae	1	0	0	1	0
Latescibacteria	Unclassified	1	1	0	1	0
Lentisphaerae	Lentisphaeria	0	0	0	0	0
	Unclassified	0	0	0	0	0
Marinimicrobia	Unclassified	0	0	0	0	0
Nitrospirae	Nitrospira	0	0	0	1	0
Parcubacteria	Parcubacteria	0	0	0	0	0
Planctomycetes	Phycisphaerae	1324	880	1417	2513	546
	Planctomycetacia	23514	11959	22743	26397	16589
	Unclassified	181	228	179	286	112
Poribacteria	Unclassified	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	38347	15829	27819	31506	19034
	Betaproteobacteria	8	7	11	13	1
	Deltaproteobacteria	810	798	867	916	1152
	Gammaproteobacteria	6213	3748	5922	5011	5119
	Hydrogenophilalia	0	0	0	0	0
	Oligoflexia	158	51	169	270	65
	Unclassified	1004	539	1114	1482	759
Rhodothermaeota	Rhodothermia	200	101	338	332	150
Spirochaetes	Spirochaetia	17	11	7	6	14
SR1	Unclassified	0	1	1	0	0
Synergistetes	Synergistia	0	0	0	0	0
Verrucomicrobia	Opitutae	20	35	22	26	34
	Spartobacteria	0	0	0	0	0
	Subdivision3	9	2	1	7	5
	Subdivision5	0	0	0	0	0
	Terrimicrobia	0	0	0	0	0
	Unclassified	60	43	61	32	43
	Verrucomicrobiae	420	222	448	564	197

Thunderbolt: Non-Corroded

Phylum	Class	DB60	DB61	DB63	DB64	DB66	DB68
Abditibacteriota	Abditibacteria	0	0	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	633	132	624	312	4456	565
	Blastocatellia	29	7	21	19	177	36
	Holophagae	0	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0	0
	Unclassified	46	25	91	26	709	76
Actinobacteria	Acidimicrobiia	668	572	488	1454	1554	1004
	Actinobacteria	3	3	0	1	71	2
	Coriobacteriia	0	0	0	0	0	0
	Nitriliruptoria	0	0	0	0	0	0
	Thermoleophilia	1	0	1	2	12	2
	Unclassified	105	35	81	119	495	168
Aminicenantes	Saccharicenantaceae	0	0	0	0	1	0
	Unclassified	0	0	0	0	0	0
Armatimonadetes	Armatimonadia	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Bacteroidetes	Bacteroidia	14	2	8	9	221	34
	Chitinophagia	23	10	9	20	12	22
	Cytophagia	2099	1169	2477	1465	5015	3465
	Flavobacteriia	3785	4295	5800	5527	9821	13912
	Saprospiria	825	135	513	513	1105	1028
	Sphingobacteriia	0	0	0	0	0	0
	Unclassified	2918	1012	1858	1165	5231	3496
Bacteria	Unclassified	4711	1970	3447	2756	11913	4154
Balneolaeota	Balneolia	13	2	5	4	6	7
Campilobacterota	Campylobacteria	0	0	0	0	2	0
Candidate Division WPS-1	Unclassified	0	6	0	2	0	2
Candidatus Saccharibacteria	Unclassified	0	0	0	0	0	1
Chlamydiae	Chlamydiia	4	0	1	0	2	0
Chloroflexi	Anaerolineae	26	30	11	17	131	104
	Caldilineae	17	21	13	24	61	37
	Chloroflexia	0	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0	0
	Thermomicrobia	0	0	0	0	4	1
	Unclassified	2	14	10	97	22	15
Cyanobacteria	Cyanobacteria	2170	15902	4799	5374	7228	21291
Deferribacteres	Deferribacteres	0	0	0	1	5	0
Deinococcus- Thermus	Deinococci	38	270	40	242	125	544
Elusimicrobia	Elusimicrobia	0	0	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0	1	0
Firmicutes	Bacilli	20	5	2	5	75	8
	Clostridia	995	277	646	488	4150	636
	Erysipelotrichia	64	42	44	22	310	74
	Negativicutes	0	0	1	0	0	0

	Unclassified	27	4	20	17	132	12
Fusobacteria	Fusobacteriia	6	2	2	12	92	7
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0	0
	Longimicrobia	0	0	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	3	0	3	2	23	0
Ignavibacteriae	Ignavibacteria	19	0	2	0	53	0
Kiritimatiellaeota	Kiritimatiellae	3	0	0	1	18	1
Latescibacteria	Unclassified	1	0	0	0	3	0
Lentisphaerae	Lentisphaeria	0	0	0	0	4	1
	Unclassified	0	0	0	0	0	0
Marinimicrobia	Unclassified	0	0	0	0	0	0
Nitrospirae	Nitrospira	1	0	0	0	2	0
Parcubacteria	Parcubacteria	0	0	0	0	0	0
Planctomycetes	Phycisphaerae	507	681	1106	628	906	1599
	Planctomycetacia	20337	15836	17296	16312	59367	23433
	Unclassified	226	98	134	121	564	156
Poribacteria	Unclassified	2	0	0	0	5	0
Proteobacteria	Alphaproteobacteria	11615	14997	18728	21255	33120	44714
	Betaproteobacteria	3	1	7	6	15	7
	Deltaproteobacteria	1461	748	1070	1382	3957	724
	Gammaproteobacteria	7498	4815	9602	6344	25497	9129
	Hydrogenophilalia	0	0	0	0	0	0
	Oligoflexia	164	124	214	82	223	179
	Unclassified	886	443	1064	608	2164	1358
Rhodothermaeota	Rhodothermia	78	50	131	200	502	442
Spirochaetes	Spirochaetia	51	1	5	6	73	2
SR1	Unclassified	0	0	0	0	0	0
Synergistetes	Synergistia	0	0	0	0	0	0
Verrucomicrobia	Opitutae	26	12	11	12	23	28
	Spartobacteria	0	0	0	0	0	0
	Subdivision3	37	4	29	5	81	23
	Subdivision5	0	0	0	0	0	0
	Terrimicrobia	0	0	0	0	0	0
	Unclassified	159	21	71	41	221	78
	Verrucomicrobiae	400	266	524	391	659	490

Corsair: Sediment

Phylum	Class	DB70	DB71	DB72	DB73
Abditibacteriota	Abditibacteria	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	1672	4098	972	617
	Blastocatellia	27	11	6	1
	Holophagae	0	0	0	0
	Thermoanaerobaculia	0	1	0	0
	Unclassified	165	454	174	44
Actinobacteria	Acidimicrobiia	461	411	251	109
	Actinobacteria	1	9	9	2
	Coriobacteriia	0	0	0	0
	Nitriliruptoria	0	0	0	0
	Thermoleophilia	8	11	5	3
	Unclassified	297	310	171	57
Aminicenantes	Saccharicenantaceae	0	48	0	0
	Unclassified	0	2	0	0
Armatimonadetes	Armatimonadia	0	0	0	0
	Unclassified	0	0	0	0
Bacteroidetes	Bacteroidia	4	59	18	13
	Chitinophagia	3	2	4	15
	Cytophagia	231	579	285	44
	Flavobacteriia	1808	1157	726	113
	Saprospiria	943	655	271	34
	Sphingobacteriia	0	0	0	0
	Unclassified	1844	2493	826	155
Bacteria	Unclassified	6477	10751	3448	1092
Balneolaeota	Balneolia	0	3	1	0
Campilobacterota	Campylobacteria	0	1	2	0
Candidate Division WPS-1	Unclassified	0	0	0	0
Candidatus Saccharibacteria	Unclassified	2	27	3	8
Chlamydiae	Chlamydiia	1	1	1	0
Chloroflexi	Anaerolineae	14	196	18	8
	Caldilineae	14	20	10	5
	Chloroflexia	0	0	0	0
	Ktedonobacteria	0	0	0	0
	Thermomicrobia	0	4	0	2
	Unclassified	3	148	4	6
Cyanobacteria	Cyanobacteria	557	358	540	265
Deferribacteres	Deferribacteres	2	96	0	0
Deinococcus- Thermus	Deinococci	106	72	26	9
Elusimicrobia	Elusimicrobia	0	0	0	0
Fibrobacteres	Chitinispirillia	0	5	0	0
Firmicutes	Bacilli	7	69	17	12
	Clostridia	138	543	385	64
	Erysipelotrichia	2	5	5	5
	Negativicutes	0	0	0	7

	Unclassified	14	185	26	8
Fusobacteria	Fusobacteriia	2	4	2	0
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0
	Longimicrobia	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	0	22	3	3
Ignavibacteriae	Ignavibacteria	2	158	6	8
Kiritimatiellaeota	Kiritimatiellae	0	36	5	6
Latescibacteria	Unclassified	3	49	3	0
Lentisphaerae	Lentisphaeria	0	0	1	0
	Unclassified	0	0	0	0
Marinimicrobia	Unclassified	0	0	0	0
Nitrospirae	Nitrospira	2	30	1	1
Parcubacteria	Parcubacteria	0	0	0	0
Planctomycetes	Phycisphaerae	142	238	60	19
	Planctomycetacia	17599	11451	9066	2994
	Unclassified	207	378	83	21
Poribacteria	Unclassified	0	0	0	0
Proteobacteria	Alphaproteobacteria	2345	2873	2280	443
	Betaproteobacteria	21	17	26	50
	Deltaproteobacteria	1588	3748	822	261
	Gammaproteobacteria	7966	9527	4309	993
	Hydrogenophilalia	0	1	0	0
	Oligoflexia	50	143	84	7
	Unclassified	964	1175	401	103
Rhodothermaeota	Rhodothermia	154	286	77	8
Spirochaetes	Spirochaetia	7	462	44	38
SR1	Unclassified	0	0	0	0
Synergistetes	Synergistia	0	0	0	0
Verrucomicrobia	Opitutae	15	16	5	4
	Spartobacteria	0	0	0	0
	Subdivision3	0	23	1	0
	Subdivision5	0	10	0	0
	Terrimicrobia	0	0	0	0
	Unclassified	195	129	54	20
	Verrucomicrobiae	195	120	102	13

Thunderbolt: Sediment

Phylum	Class	DB74	DB75	DB76	DB77
Abditibacteriota	Abditibacteria	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	6027	1747	2115	2247
	Blastocatellia	116	23	26	11
	Holophagae	0	0	0	0
	Thermoanaerobaculia	0	0	0	0
	Unclassified	391	119	155	201
Actinobacteria	Acidimicrobiia	827	783	574	268
	Actinobacteria	86	2	5	8
	Coriobacteriia	3	0	0	0
	Nitriliruptoria	0	0	0	0
	Thermoleophilia	44	3	4	4
	Unclassified	798	614	516	235
Aminicenantes	Saccharicenantaceae	0	0	0	5
	Unclassified	0	0	0	0
Armatimonadetes	Armatimonadia	6	0	1	0
	Unclassified	2	0	0	4
Bacteroidetes	Bacteroidia	188	9	49	31
	Chitinophagia	49	4	4	4
	Cytophagia	543	133	251	312
	Flavobacteriia	3704	837	911	720
	Saprospiria	2797	363	572	567
	Sphingobacteriia	8	0	0	0
	Unclassified	3068	363	743	1155
Bacteria	Unclassified	14334	3146	4500	4906
Balneolaeota	Balneolia	0	0	0	0
Campilobacterota	Campylobacteria	0	0	0	0
Candidate Division WPS-1	Unclassified	20	0	0	0
Candidatus Saccharibacteria	Unclassified	3	0	0	7
Chlamydiae	Chlamydiia	0	0	2	0
Chloroflexi	Anaerolineae	24	8	34	57
	Caldilineae	11	9	9	10
	Chloroflexia	0	0	0	0
	Ktedonobacteria	1	0	1	0
	Thermomicrobia	2	0	4	1
	Unclassified	10	2	10	29
Cyanobacteria	Cyanobacteria	455	1640	780	397
Deferribacteres	Deferribacteres	6	0	2	22
Deinococcus- Thermus	Deinococci	97	58	58	43
Elusimicrobia	Elusimicrobia	0	0	0	0
Fibrobacteres	Chitinispirillia	0	0	0	0
Firmicutes	Bacilli	116	20	8	24
	Clostridia	251	109	341	557
	Erysipelotrichia	15	8	21	32
	Negativicutes	88	0	0	0

	Unclassified	24	21	35	96
Fusobacteria	Fusobacteriia	32	0	4	2
Gemmatimonadetes	Gemmatimonadetes	18	0	0	0
	Longimicrobia	2	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	14	6	6	13
Ignavibacteriae	Ignavibacteria	5	0	20	36
Kiritimatiellaeota	Kiritimatiellae	1	0	12	10
Latescibacteria	Unclassified	2	0	6	24
Lentisphaerae	Lentisphaeria	1	0	0	0
	Unclassified	0	0	0	0
Marinimicrobia	Unclassified	0	0	0	0
Nitrospirae	Nitrospira	23	0	8	9
Parcubacteria	Parcubacteria	0	0	0	0
Planctomycetes	Phycisphaerae	218	66	89	84
	Planctomycetacia	28096	19533	18081	10411
	Unclassified	836	167	206	238
Poribacteria	Unclassified	0	0	0	0
Proteobacteria	Alphaproteobacteria	3658	1444	1780	1998
	Betaproteobacteria	264	57	60	17
	Deltaproteobacteria	5306	1026	1630	2229
	Gammaproteobacteria	21580	3973	6519	5822
	Hydrogenophilalia	0	0	0	0
	Oligoflexia	88	21	83	55
	Unclassified	1741	515	697	619
Rhodothermaeota	Rhodothermia	446	87	124	191
Spirochaetes	Spirochaetia	16	2	59	128
SR1	Unclassified	0	0	0	0
Synergistetes	Synergistia	0	0	0	0
Verrucomicrobia	Opitutae	25	4	6	15
	Spartobacteria	4	0	0	0
	Subdivision3	6	0	0	7
	Subdivision5	0	0	2	1
	Terrimicrobia	2	0	0	0
	Unclassified	121	22	26	43
	Verrucomicrobiae	300	108	137	98

Seawater: Corsair (DB78-80) and Thunderbolt (DB81-83)

Phylum	Class	DB78	DB79	DB80	DB81	DB82	DB83
Abditibacteriota	Abditibacteria	0	0	0	0	0	0
Acidobacteria	Acidobacteria, Gp1-9	34	13	20	54	37	54
	Blastocatellia	4	1	3	1	1	0
	Holophagae	0	0	0	0	0	0
	Thermoanaerobaculia	0	0	0	0	0	0
	Unclassified	6	2	2	3	5	6
Actinobacteria	Acidimicrobiia	98	42	68	23	9	18
	Actinobacteria	32	0	7	14	8	11
	Coriobacteriia	0	1	0	0	0	1
	Nitriliruptoria	0	0	0	0	0	0
	Thermoleophilia	0	0	0	0	0	0
	Unclassified	64	38	96	23	13	14
Aminicenantes	Saccharicenantaceae	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Armatimonadetes	Armatimonadia	0	0	0	0	0	0
	Unclassified	0	0	0	0	0	0
Bacteroidetes	Bacteroidia	191	73	129	154	84	92
	Chitinophagia	228	257	0	40	2	2
	Cytophagia	1299	751	891	141	97	127
	Flavobacteriia	25664	15640	18357	40324	43776	34604
	Saprospiria	99	43	69	88	70	66
	Sphingobacteriia	0	0	0	0	1	0
	Unclassified	9257	4777	5657	9034	18950	16968
Bacteria	Unclassified	6445	3302	4530	2018	1483	1416
Balneolaeota	Balneolia	61	58	64	4	5	3
Campilobacterota	Campylobacteria	2	3	3	6	6	1
Candidate Division WPS-1	Unclassified	0	0	0	0	0	0
Candidatus Saccharibacteria	Unclassified	0	2	0	0	3	0
Chlamydiae	Chlamydiia	0	0	0	1	3	0
Chloroflexi	Anaerolineae	3	0	2	5	0	0
	Caldilineae	1	1	1	0	1	0
	Chloroflexia	0	0	0	0	0	0
	Ktedonobacteria	0	0	0	0	0	0
	Thermomicrobia	0	0	0	1	0	0
	Unclassified	0	1	0	0	0	2
Cyanobacteria	Cyanobacteria	58133	31635	36104	15656	16338	19262
Deferribacteres	Deferribacteres	0	0	1	1	0	2
Deinococcus-Thermus	Deinococci	23	8	4	7	4	5
Elusimicrobia	Elusimicrobia	0	0	0	0	1	0
Fibrobacteres	Chitinispirillia	0	0	0	0	0	0
Firmicutes	Bacilli	22	4	3	179	50	46
	Clostridia	121	51	95	161	59	75
	Erysipelotrichia	13	8	16	44	9	18
	Negativicutes	0	0	1	1	12	5

	Unclassified	7	0	2	11	8	1
Fusobacteria	Fusobacteriia	140	61	51	77	49	48
Gemmatimonadetes	Gemmatimonadetes	0	0	0	0	0	0
	Longimicrobia	0	0	0	0	0	0
Hydrogenedentes	Candidatus Hydrogenedens	0	0	0	1	0	3
Ignavibacteriae	Ignavibacteria	0	0	0	0	0	0
Kiritimatiellaeota	Kiritimatiellae	190	135	200	2	1	7
Latescibacteria	Unclassified	0	0	0	0	0	0
Lentisphaerae	Lentisphaeria	10	1	2	5	1	2
	Unclassified	2	0	0	0	0	0
Marinimicrobia	Unclassified	434	292	262	1	0	0
Nitrospirae	Nitrospira	0	0	1	2	1	6
Parcubacteria	Parcubacteria	0	0	0	0	0	0
Planctomycetes	Phycisphaerae	25	10	20	66	63	54
	Planctomycetacia	931	461	722	618	239	274
	Unclassified	108	54	83	24	13	22
Poribacteria	Unclassified	0	0	0	0	0	0
Proteobacteria	Alphaproteobacteria	43157	25336	35171	45648	41898	35476
	Betaproteobacteria	2206	1732	196	427	306	225
	Deltaproteobacteria	156	51	110	178	91	107
	Gammaproteobacteria	5704	3439	4186	2882	3160	2860
	Hydrogenophilalia	0	0	0	0	0	0
	Oligoflexia	60	50	86	225	161	191
	Unclassified	2288	1342	1822	5664	4013	3771
Rhodothermaeota	Rhodothermia	8	3	13	25	20	26
Spirochaetes	Spirochaetia	4	3	4	4	15	7
SR1	Unclassified	0	0	0	1	0	1
Synergistetes	Synergistia	1	0	1	3	0	0
Verrucomicrobia	Opitutae	148	79	117	18	11	14
	Spartobacteria	0	0	0	0	0	0
	Subdivision3	14	5	5	1	2	1
	Subdivision5	0	1	1	0	0	0
	Terrimicrobia	0	0	0	0	0	0
	Unclassified	4	0	4	1	4	4
	Verrucomicrobiae	255	91	162	116	90	93