



Shifting Baselines to Thresholds: Reframing Exploitation in the Marine Environment

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Current research on anthropogenic impacts on marine ecosystems often relies on the concept of a “baseline,” which aims to describe ecosystems prior to human contact. Recent research is increasingly showing that humans have been involved in marine ecosystems for much longer than previously understood. We propose a theoretical framework oriented around a system of “thresholds” referring to system-wide changes in human culture, ecosystem dynamics, and molecular evolution. The concept of the threshold allows conceptual space to account for the fluid nature of ecosystems throughout time while providing a critical framework for understanding drivers of ecosystem change. We highlight practical research approaches for exploring thresholds in the past and provide key insights for future adaptation to a changing world. To ensure ecological and societal goals for the future are met, it is critical that research efforts are contextualized into a framework that incorporates human society as integral to ecology and evolution.

Keywords: ecology, ancient biomolecules, evolution, conservation, thresholds, sustainability

FROM BASELINES TO THRESHOLDS

Humans have long been part of marine ecosystems worldwide, although the nature of this relationship has changed over time and space. Today many marine ecosystems are deeply threatened, including commercial fish stocks, coral reefs, and polar environments (Bindoff et al., 2019; Worm and Lotze, 2021). The ongoing crisis in the world’s oceans threatens vulnerable species and ecosystems as well as economic stability and food security (FAO, 2018). Further, the world is shifting toward relying even more heavily on the ocean (Costello et al., 2020). From these trends, it is clear that research must address the maintenance of ocean ecosystems. To balance the various needs of all ecosystem actors, both human and non-human, it is crucial that we have language and theory that reflects the dynamic nature of marine ecosystems and our place in them.

Addressing the problem of ocean ecosystem degradation requires enormous interdisciplinary effort. This effort, however, is often stymied by the way in which knowledge creation occurs in marine science. In 1995, Daniel Pauly published a paper on the now-famous phenomenon known as “shifting baselines syndrome (SBS),” in which collective environmental knowledge and memory move forward in time with successive generations, resulting in gradual loss of knowledge regarding the previous state of an ecosystem (Pauly, 1995). Continuous environmental degradation can result in a misinterpretation of changes over time, frequently leading to under-valuation of environmental carrying capacities or species population sizes (Lotze and Worm, 2009; Rodrigues et al., 2019) making researchers ill-equipped to fully understand changing ecosystems. Yet, the environments

being studied have been transformed by human actions, often for a much longer time period than is commonly assumed (Lotze and Worm, 2009; Rodrigues et al., 2019).

Although the prevalence of SBS has been clearly demonstrated, the concept itself relies on a problematic ecological assumption: that there is a “baseline” for any one species or ecosystem dynamic. This implies a singular, natural state for any particular ecosystem, which, in practice, becomes fraught with arbitrary decisions regarding how a “baseline” is determined (Lotze and Worm, 2009; Rodrigues et al., 2019). To illustrate this point, Collins et al. (2020) estimated historical population sizes of hunted North American mammals throughout history using two different historical time points as cut-offs for baseline calculation. They found that by pushing the timeline back 100 years, population size estimates increased by over 10%, suggesting the original estimates were likely misleading due to the arbitrary designation of a temporal baseline. Such studies are crucial in illustrating the arbitrary nature of baseline determination while acknowledging the equally important role baseline assumptions play in knowledge creation.

It is clear that humans have had a significant and deleterious effect on our surrounding ecosystems in our more recent history. Yet, it is also important to emphasize that humans have played a role in our environments for the entirety of our evolutionary history, including coastal and marine ecosystems (Rick and Erlandson (eds), 2008; Stringer et al., 2008). This role was neither inherently positive nor inherently negative our long relationship with the marine environment and the increasingly appreciated dynamic nature of ecosystem stability illustrates the fact that the “baseline” concept itself is what should be shifting. Rather than focusing on a baseline, the concept of SBS should be incorporated into a wider theoretical framework of thresholds in marine environments which explicitly incorporates human culture as an integral component of marine ecosystems. As will be discussed below, the concept of the threshold allows conceptual space for the fluid nature of ecosystems throughout time. It also provides markers for establishing baselines and a critical framework for understanding drivers of ecosystem change.

By incorporating SBS into a larger discussion of thresholds, the debate can be shifted back to understanding long-term ecosystem dynamics rather than elucidating concrete baselines. Further, the concept of thresholds expands the timescale further than that of SBS, allowing complete incorporation of ecological and evolutionary dynamics into the discussion of sustainable resource management. Finally, as we will show, SBS can be conceptualized as a key component within the wider threshold structure as a cultural characteristic that facilitates the crossing of a certain type of threshold—the tipping point.

We recognize that some of these concepts have been previously addressed in other studies and reviews (Groffman et al., 2006; Samhouri et al., 2010; Rodrigues et al., 2019). Here, we propose a framework that seeks not to disprove other attempts but to expand and enhance inquiry into past ecosystems. We propose a generalized research approach. We emphasize the way in which recent advances in molecular research can illuminate long-term ecosystem change when they are firmly grounded in theory that explicitly incorporates human

society in our understanding of what constitutes an “ecosystem.” We situate this framework within previous theoretical work, including SBS. We then highlight knowledge gaps in ecological and evolutionary thresholds that can be addressed through biomolecular methods that have become increasingly efficient and accessible in recent years, such as genomics and palaeo-/archaeo-genomics and stable isotopes analysis. Finally, we provide suggestions for future research and the impact such studies could have on providing crucial information for future environmental resource management.

DEFINING THRESHOLDS IN MARINE ECOSYSTEMS

The technical definition of a “threshold” in the *Oxford English Dictionary* is, “[t]he magnitude or intensity that must be exceeded for a certain reaction or phenomenon to occur” (OED, 2021). We use this definition of “threshold” to define various subtypes of threshold that are relevant for understanding marine ecosystems: the magnitude or intensity of some *driver* increases or decreases to the point that a *threshold* is crossed. Here we highlight three major threshold categories that pertain to change in marine ecosystems: *cultural*, *ecological*, and *evolutionary* (see **Table 1**) and discuss various research techniques to identify when a threshold has been crossed, e.g., a certain reaction or phenomenon has occurred. For each category, threshold identification is always dependent on the research question: it relies on the reaction or phenomenon of interest in the study.

When discussing marine resource exploitation, there are several major ways in which a threshold can be identified. The first is to pinpoint times in the past at which human societies experienced a major transition that coincided with changes in relationships to marine ecosystems: *thresholds in culture*. These thresholds are based on phenomena such as changes in perception of marine environments, technological loss/innovation, economic development, and changes in resource use fall into this category. Thresholds in culture signify a shift in human society that impacts societal-level relationships with the surrounding environment. There are several cultural thresholds that have been identified in human history and are widely known, including the Neolithic and Industrial “revolutions” and the rise of the Information Age. It should be noted, however, that shorter or seemingly less dramatic periods of flux can also be considered cultural thresholds though this is dependent on the scale of the study and the research question. Some examples of cultural thresholds include religious change, technological advance, and political regime changes (including societal collapse). These changes often affect the relationship between humans and their environments, even if indirectly, through changing subsistence patterns, access to novel food sources through trade, and changing economic and political regulations. Cultural thresholds that impact human exploitation in the marine environment are varied and often relate to technological advance (e.g., seafaring technology or improved fishing techniques) (Unger, 1980; Couper, 2009; O’Connor et al., 2011; Montenegro et al., 2016), but can also be linked to cultural mores surrounding

seafood consumption, as seen with the arrival of Christianity in northern Europe and the associated increase in fish consumption on religious holidays in lieu of meat (Hoffmann, 2001, 2005; Müldner and Richards, 2005). Although these cultural changes can (and often do) have ecological implications, impacting the ecology is not a requirement for a cultural threshold.

The second category of thresholds characterizes ecosystem boundaries according to species biology or ecological traits. These are *thresholds in ecology*. Thresholds in ecology encompass relationships between species in an ecosystem (e.g., mutualism, predation, symbiotic relationships, trophic balance, etc.) and can refer to radical shifts in ecosystem dynamics as a whole. Again, the threshold is scalable depending on the research aims. Thresholds in ecology can be linked to anthropogenic impacts but may also occur naturally, such as in the process of ecosystem turnover. Thresholds in ecology can also be driven by abiotic factors, both extrinsic, such as the introduction of pollutants or chemicals, and intrinsic, such as biogeological processes like shifting currents and changes in upwelling. Such ecological thresholds are commonly used in exploitation policies today. For example, fisheries policies are often based on measures of spawning-stock biomass—the number of fish in a species that can reproduce in any given year—requiring that human extraction levels do not cause the population to dip below a certain threshold based on the minimum remaining stock size calculated for sustaining the population (De Lara et al., 2007). We here avoid the terms “ecosystem services” and “ecosystem function” as these have been used in the past to create hierarchies between human societies and their surrounding ecosystems and frame management goals purely in terms of how these ecosystems can benefit humans (de Groot, 1987; de Groot et al., 2002; Costanza et al., 2017). We recognize that the definition of the term “ecosystem function” has been under debate in ecological research for some time (Paterson et al., 2012). As it can be used as an underpinning for determining ecosystem services and occasionally synonymously with “ecosystem services” (e.g., Peterson et al., 2010; Oliver et al., 2015; Hillman et al., 2018), we choose to avoid this term altogether.

Finally, there are *thresholds in evolution*. Evolutionary thresholds are crossed when there is a heritable change in genotype or phenotype in a species. For simplicity's sake, we here discuss molecular evolution as the main example for crossing and evolutionary threshold. This includes demographic shifts such as bottlenecks and population expansions, selective processes and inbreeding, and other phylogenomic phenomena. Potential drivers of threshold crossing include: species migration, climate change, and abiotic factors such as ocean acidification and temperature changes. In recent history, many of these thresholds are likely reached due to human activity, but may have been non-anthropogenic in the past. In this paper, we focus on human exploitation as a critical example of how anthropogenic change can induce an evolutionary threshold. For example, the concept of fisheries-induced evolution postulates that intensive fishing pressures cause an evolutionary change in fish species, mostly by changing life-history traits for faster maturation (Heino et al., 2015; Pinsky et al., 2021). Fisheries-induced evolution occurs when fishing has reached a scale in which evolution is impacted,

which may be temporally decoupled from the ecological or cultural thresholds.

Recent discourse in ecosystem management, on anthropogenic impacts on the environment, and on climate change has revolved around the notion of maintaining human activity and ecosystem dynamics within a set of sustainable boundaries often referred to as “thresholds” or “tipping points” (Lenton and Schellnhuber, 2007; Rockström et al., 2009; Russill and Nyssa, 2009). As these terms are not often concretely distinguished, we suggest a differentiation between them. A threshold is distinct from a “tipping point” in that it does not inherently imply a system that has lost crucial regulatory elements. A tipping point can be a form of a threshold, but thresholds exist which are not “tipping points.” For example, quantification of sprat population size dynamics has revealed distinct thresholds at which the Baltic Sea ecosystem transitions to an alternate stable state (Casini et al., 2009) but the overall ecosystem dynamics remain unchanged. In contrast, extractivist policies based on research generated under SBS is a cultural characteristic that is causing our oceans to hurtle toward global fisheries collapse and near-total ecosystem degradation (Pauly, 1995; Jackson et al., 2001; Roberts, 2007; Bindoff et al., 2019), therefore is key to crossing the tipping point. Crossing this threshold would be nothing short of catastrophic, which only serves to highlight the importance of deepening our understanding of the other three thresholds. Establishing how thresholds in culture, ecology, and evolution are crossed is therefore of crucial importance to better inform ecosystem management efforts and foster novel approaches to avoid tipping points.

Although seemingly straightforward in definition, these thresholds are in practice entwined in complex, interdependent relationships. For example, advances in fishing technology constitute not only a cultural threshold, but also ecological and evolutionary thresholds as selective fishing and its ecological impact will act as new elements in the marine environment, e.g., with the advent of deep-sea trawling. Given the complexity of human behavior, ecosystem dynamics, and species evolution, it is critical to explore these thresholds thoroughly both in conjunction and as separate phenomena. It can be difficult to determine at what point a threshold has been crossed or what should be considered a “threshold.” The threshold concept is not one-size-fits-all, rather it is a flexible approach that can be scaled across time and space.

DETERMINING THRESHOLDS: A GENERALIZED APPROACH

Here, we lay out the ideal workflow for addressing the issue of identifying thresholds in marine ecosystems in the context of marine resource exploitation. First, context must be grounded in historical, paleontological, archeological, and anthropological research. This includes consultation of historical records, archeological site reports, and, where applicable, ethnographies. Critically, what this means for ecologists is directly searching for answers to ecological/evolutionary questions outside the field

of ecology. A strong background in the relevant historical and archeological contexts of the time period and/or biological system in question shifts ecological inquiry away from assumptions that long-term change must be caused by abiotic factors, such as climate, whereas only recent changes can be due to human activity in the ecosystem. Concurrently, a relevant background in the natural history of the biological system in question is crucial for framing the historical and archeological context. Biomolecular analysis can then be carried out. This work must be situated in archeology, history, indigenous knowledge, and ecology in order to interpret results in a nuanced approach based in systems-level thinking.

Archeology, anthropology, and historical research are key methodological approaches with which to explore cultural thresholds. The application of these methods, however, are not stand-alone modes of inquiry into the problem of identifying sustainable practices. Research must be framed in the context of archeology, history and, wherever applicable, indigenous knowledge. Incorporating all types of knowledge is the only way we will be able to balance issues such as food security with the pressing problems of declining biodiversity, climate change, and social justice.

Many studies of marine resource extraction set their baseline as the mid- or early twentieth century, citing a drastic change in technology that allowed for increased fishing capacity in hitherto inaccessible regions of the globe (Pinnegar and Engelhard, 2008). This is, of course, an important cultural threshold in marine resource extraction and one that merits attention. It is likely, however, that industrial-scale exploitation was occurring, for at least some populations, much earlier than the twentieth century. In the Atlantic, archeological and historical research has revealed fisheries on an enormous scale occurring up to 1,000 years ago (Barrett, 2019). Indeed, Barrett et al. (2004) propose that a cultural threshold was crossed at this time in the form of the “Fish Event Horizon,” in which the English proto-industrial fishing operations reached a high enough level that the surrounding North Sea ecosystems were forever changed. These conclusions were reached based on zooarchaeological analysis in combination with analysis of historical documents, suggesting that the mid- or early twentieth century baselines established for many marine populations are again subject to SBS. This illustrates the capacity of archeological and historical research to exhibit thresholds in human culture that indicate likely parallel ecological thresholds. While providing significant insights, these sources remain limited for generating a comprehensive understanding of the marine ecosystem. Archeological and historical research efforts are adept at determining thresholds in human behavior such as major societal changes or shifts in scale of exploitation, yet both are less well-equipped for informing us about species or ecosystem dynamics (Barrett, 2019; Oosting et al., 2019).

Molecular analysis of archeological assemblages, undertaken in collaboration with archeologists and historians, can provide novel insight into broader ecological questions. These approaches include stable isotope analysis, proteomics, and genomics, often in conjunction with archeology and paleontology to form the discipline of biomolecular archaeo/paleontology. The research aims that can be addressed include: species

identification (Biard et al., 2017); establishing trade, migration, and population continuity (Star et al., 2017); reconstructing demographic history and evolutionary change (De Bruyn et al., 2009; Foote et al., 2013); and analyzing past ecological and climatic conditions (Gokhman et al., 2017). Recent advances in ancient biomolecular techniques have created a novel arena for investigating thresholds, one that is already beginning to take shape in bioarchaeology and marine ecology (Martínez-García et al., 2021; Ólafsdóttir et al., 2021). By reconstructing past ecosystems using ancient DNA and stable isotope analysis, it may be possible to observe periods of stability and flux, providing a better understanding of what constitutes a balanced and sustainable ecosystem in support of future-oriented conservation efforts. Indeed, ecological principles identified through molecular approaches could provide policymakers and scientists with the knowledge necessary to not only recover damaged ecosystems but to help foster novel ecosystems in the coming years (Alagona et al., 2012; Mániez et al., 2014).

We recognize that such an approach to inquiry requires generalized knowledge and a strong collaborative research network that draws on expertise in each of these fields. In recent years, such networks have been established in marine ecology (e.g. Oceans Past Initiative, 2021; Sea Change Project, 2021; SeaChanges Itn, 2021). We anticipate that as the field turns toward incorporating social science and humanities, we will see an influx of networks of this type increasing.

Determining Thresholds: Molecular Methods

Molecular methods in thresholds analysis often take the form of biomolecular archeology. This typically involves collecting remains from archeological sites, such as bones or other preserved tissue, to extract informative molecules from these samples. Although traditional morphological studies are typically used to understand faunal assemblages from archeological sites, molecular approaches can provide novel insight into broader ecological questions. To illustrate the potential of biomolecular archeology for research on marine thresholds, we highlight the fields of palaeogenomics and stable isotope analysis as well as the emerging field of palaeoproteomics to illustrate the power of biomolecular archeology to provide crucial information for research into marine thresholds.

Palaeogenomics

The field of palaeogenomics has come into its own in the last decade with the accessibility of ancient DNA laboratories and genomic sequencing techniques (Dabney et al., 2013). This has allowed the field to conduct molecular analysis to a scope that was previously not possible with the prior limited capacity for ancient genome sequencing, opening up new applications for ancient DNA (Rawlence et al., 2021 and references therein). Since then, ancient DNA has been extensively used to explore the relationship between humans and animal species, both wild and domesticated, mainly focused on large terrestrial land mammals and hominids (Meyer, 1992; Dabney et al., 2013; Druzhkova et al., 2013; Woods et al., 2018). However, remains from fish, marine mammals, and other aquatic species are often recovered from

archeological sites and included in zooarchaeological analyses. This large corpus of predominantly unanalyzed material from marine animals should not be overlooked.

Molecular approaches can bypass many of the limitations of traditional zooarchaeological analysis and provide key insight on issues such as species identification (Biard et al., 2017; Rodrigues et al., 2018), establishing origin (Star et al., 2017), and demographic history (Nye et al., 2020). Similar methodologies have been extensively employed to research domesticates, large prehistoric mammals, and humans (Green et al., 2010; Lorenzen et al., 2011; Meyer et al., 2012; Librado et al., 2017; MacHugh et al., 2017). However, palaeogenomic analysis is far less frequently applied to marine populations, particularly those heavily exploited by humans, both past and present (Oosting et al., 2019). In the last few years, the use of ancient marine samples has begun to increase as laboratory techniques for such samples have improved (Boessenkool et al., 2017; Der Sarkissian et al., 2020; Ferrari et al., 2021b; Martínez-García et al., 2021).

The use of aDNA and reconstructive genomics can provide a deeper time scale than historical catch records. With new bioinformatic techniques, ancient genetic data integrate seamlessly with modern data (Ferrari et al., 2021a; Speidel et al., 2021), for instance allowing temporal assessments of overall population size or population of origin, something that is challenging to achieve using traditional archeological and historical methods (Star et al., 2017; Smith B.T. et al., 2021; van der Valk et al., 2021). By reconstructing past ecosystems using ancient DNA, it may be possible to see changing relationships between human society and the marine ecosystem, thereby providing a better understanding of what constitutes a sustainable ecosystem and key tools for future-oriented conservation efforts. For example, Welch et al. (2012) successfully applied ancient DNA analysis to identify local extirpations in the endemic Hawaiian petrel, illustrating range contraction of the species over time and providing guidance for future conservation efforts. Similar approaches have been used to identify possible source populations for reintroducing Eurasian beavers to the United Kingdom (Marr et al., 2018). By establishing a time series of population dynamics that is hundreds to thousands of years old, it is, for the first time, possible to clarify long-term evolutionary trends for exploited populations and their likely drivers, whether those drivers be anthropogenic or otherwise.

Ancient DNA can also be used to identify cultural patterns, which could help elucidate past cultural thresholds. For example, studies of dental calculus—calcified plaque on tooth remains—is a treasure trove of information on the ancient oral microbiome (Warinner et al., 2015). Analysis of dental calculus in human remains has revealed information on past diets, medicinal use, and ancient dental practices and associated cultural shifts (Blatt et al., 2011; Adler et al., 2013; Warinner et al., 2014; Sawafuji et al., 2020). As of yet no studies specifically link dental calculus to marine exploitation, but that does not preclude its potential applicability to understanding changing marine resources. Ancient genomes can also be used to trace patterns of human migrations and associated changes in land use and subsistence (Racimo et al., 2020). Past patterns of human migration are often

linked to cultural and/or biological replacement of pre-existing populations (Li et al., 2014), indicating large cultural thresholds could be crossed during periods of mass migration. Modern genomic sequences are often used to study past migrations to great effect (Leslie et al., 2015). Yet, the addition of ancient DNA can provide time-calibrations and an extended window into the past for some of these migrations that greatly alters our understanding of past cultures (Margaryan et al., 2020). These examples, which document Viking expansion into the islands that include the present-day United Kingdom and Ireland, can be used to assess past cultural relationships with the sea, as Viking culture is well-known to have been dependent in large part on marine subsistence, in contrast to some of the populations they conquered (Naumann et al., 2014).

It is often assumed that humans entering a new environment irrevocably change the ecosystem and, thus, efforts for “rewilding” or restoration rely on the premise that whatever existed prior to human interaction is the “natural” state of the ecosystem. Emerging evidence from palaeogenomic studies shows that, while humans have of course changed marine environments, the narrative that drives the human-ecosystem binary is over-simplifying the true state of ecosystem dynamics. For example, the Grand Banks Atlantic cod population famously collapsed in the 1990s, to the devastation of local communities (Myers et al., 1997). The cod population has still not rebounded, resulting in a trophic cascade around the Newfoundland coast (Frank et al., 2005; Neuenhoff et al., 2019). Yet, recent analysis has shown that, despite the severe population bottleneck the Atlantic cod population has suffered in the last few decades, their genetic diversity remains stable and, thus, old phenotypes and ecosystem dynamics may still be recovered (Pinsky et al., 2021). Studies such as this challenge the long-held assumption that intense exploitation of fisheries must inherently result in evolutionary threshold-crossing on the species-level and emphasize that there are pathways forward for maintaining human-marine relationships that allow both sustainable interaction and exploitation of marine resources and balancing ecosystem dynamics. Similar studies have shown that genetic diversity is robust to periods of intense human exploitation in various species (Welch et al., 2012; Pajmans et al., 2020; Martínez-García et al., 2021).

These studies highlight the importance of not conflating different thresholds. Ecological thresholds were crossed in the Grand Banks as the ecosystem shifted to an alternate stable state, yet genomic results show that molecular evolutionary thresholds have not yet been crossed. Further, they illustrate that while cultural thresholds in exploitation may be informative for identifying ecological and evolutionary thresholds, one must be sure not to project cultural thresholds onto the environment as points of no return. The example of the Grand Banks cod industry also highlights the importance of scale in determining thresholds. At the regional level, the Grand Banks cod population seems to be on the cusp of recovery, as illustrated above. Yet, in some locations an ecological tipping point threshold has, indeed, been passed even if a molecular extinction threshold has not been shown, with local populations in some areas heading quickly toward

TABLE 1 | The three thresholds.

Threshold	Definition	Examples of drivers	Examples of thresholds
Cultural	Major societal transitions that coincide with changes in relationships to marine ecosystems, often resulting in changed societal perception and use of nature and/or marine environments	The invention of trawling; the Industrial Revolution; Animal domestication events; Onset of the North American Fur Trade; The invention of motorized vessels	Dietary change; Economical shift; Urbanization of coastal areas
Ecological	A boundary in ecosystem dynamics that results in a balance shift within and/or between ecosystems. This can occur at the inter- and intra-species level or be related to abiotic factors	Glacial Periods; Climate Change; Extirpation events; Population density of particular species; Onset of pollution	Species richness; trophic interactions; populations connectivity; distribution of species; historical population size
Evolutionary	A heritable change in a species' genotype or phenotype that impacts a population larger than a single lineage	Growth/reductions in population size; Isolation; Changes in sexual selection; adaptation to environmental changes	The evolution of lactase persistence in humans; Creation of domesticated animal species/breeds; adaptive potential; accumulation of deleterious mutations; diversity gain or loss

extirpation (Swain et al., 2015, 2019). This illustrates the necessity of identifying thresholds across different geographic and ecological scales and the interplay between thresholds at various levels. There could, for instance, be an evolutionary or ecological threshold that is crossed at the species or regional level when enough local thresholds have been crossed. This is in line with the traditional emphasis in conservation genomics to preserve local populations for species-wide diversity and adaptive potential through techniques like genetic rescue (Supple and Shapiro, 2018).

Stable Isotopes

Stable isotopes analysis has, much like DNA, been an increasingly accessible tool for archeologists and ecologists alike over the last several decades. Stable isotopes of animal tissue are typically used for analysis of trophic level, dietary reconstruction and foraging ecology, migration, and habitat use. In archeology, stable isotope analysis has been primarily applied to human bone samples. The majority of these studies rely on carbon and nitrogen stable isotope analysis to reconstruct diet, often focused on identifying agricultural transitions (Lee-Thorp, 2008; Sponheimer et al., 2013; Hu, 2018). Other stable isotopic systems including sulfur and oxygen have also been applied to studies of human remains to examine diet (Nehlich et al., 2012; Rand and Nehlich, 2018) and migration (Prowse et al., 2007; Leach et al., 2009; Guo et al., 2018). Applications to past human cultures, particularly those that highlight changing diets and migration, can provide important insights into past cultural thresholds, such as changing religious practices, political regimes, or technological advance that resulted in altered subsistence patterns (Kosiba et al., 2007; Ventresca Miller et al., 2014; Alexander et al., 2019; Cheung et al., 2019). Dietary reconstruction of human populations can identify the incorporation (or lack thereof) of marine resources in the diet (typically requiring a consistent level of consumption over a sustained period) (Goude et al., 2017; McConnan Borstad et al., 2018; Tung and Knudson, 2018). Stable isotopic analysis is increasingly being applied to zooarchaeological remains providing a unique window into the past which can be used to compare to modern ecological studies (Pilaar Birch, 2013). These studies often focus on animal domestication (Hu et al., 2014), seasonality of birth (Frémondeau et al., 2015;

Tornero et al., 2016), and husbandry practices (Cucchi et al., 2016; Manin et al., 2018; Bishop et al., 2020).

In marine systems, stable isotopes have provided proxies for changes in water temperature, salinity, nutrient sources, and food-web complexity (Geffen et al., 2011; Barrett, 2019). Carbon and nitrogen stable isotope analysis have been used to understand foraging ecology (McClellan et al., 2010; Newsome et al., 2010; Szpak et al., 2018, 2019). Due to differences in isotopic discrimination, there are benthic-pelagic differences in $\delta^{13}\text{C}$ values, which results in inshore foragers exhibiting higher $\delta^{13}\text{C}$ values than offshore species (Hobson et al., 1997; Cherel and Hobson, 2007; Andersen et al., 2021). For example, Ólafsdóttir et al. (2021) used zooarchaeological remains associated with Icelandic demersal fisheries to explore the impact of increasing fishing pressure on the trophic levels of Atlantic cod, haddock, and wolffish. By explicitly linking this research to historical and archeological research into the development of the proto-industrial cod fishery in the Medieval era, they were able to compare isotopic signatures over the last 700 years to modern signatures, revealing a strong sign that fishing pressures have both lowered the trophic level for species like cod and resulted in convergence on a single trophic niche for demersal fishes in this environment. Other isotopic systems have also been used, including sulfur as a proxy for foraging ecology (Szpak and Buckley, 2020) and zinc for trophic level in archeological arctic marine mammal bone (Jaouen et al., 2016; McCormack et al., 2021). Oxygen isotopes in marine systems have been used to identify habitat use (Clementz and Koch, 2001; Drago et al., 2020). Guy et al. (2018) used oxygen isotopes to identify fish from a hypersaline lagoon environment in northern Egypt and are able to identify a period of intense exploitation, and trade based on the isotopic signature.

Stable isotope analysis often relies on proxies for data collection. For example, using an innovative approach based on extracting isotopes from ocean quahog, Estrella-Martínez et al. (2019) were able to reconstruct recruitment estimates for the North Sea herring population. Using a marine historical ecology approach, they then cross-checked these estimates with historical resources regarding fishing pressure and catch-per-unit-effort over time. This sort of approach highlights the current ability of molecular research to transform our understanding of the

interplay between humans and the marine environment. Further, it emphasizes the ability to conduct systems-level analysis (they primarily wanted to investigate primary productivity) from a single isotopic signature when this signature is fully grounded in historical and archeological context.

Palaeoproteomics

Ancient DNA is an incredibly powerful tool for illuminating past evolutionary dynamics. However, it is dependent on well-preserved specimens, often restricting research both temporally and geographically (Hofreiter et al., 2014). In contrast to fragile DNA sequences, which begin to degrade immediately post-mortem, proteins are more stable molecules that are less susceptible to degradation over time (Collins et al., 2010). Palaeoproteomics, the extraction of ancient protein molecules from paleontological and archeological remains, is an alternative, minimally destructive method that can also be used on older and less-well-preserved specimens (Welker, 2018). Emerging techniques based on well-established proteomics methods, such as Zooarchaeology by Mass-Spectrometry (ZooMS) can provide taxonomic identification of poorly preserved specimens at relatively low costs without destructive sampling (Buckley et al., 2009; Collins et al., 2010; van Doorn et al., 2011) and provide information for phylogenetic analysis (Welker et al., 2016; Welker, 2018).

Compared to the previously mentioned methods, palaeoproteomic methods are under-developed. Yet, they are still able to shed light on past societal trends of marine resource use, and biological and ecological trends, e.g., shifts in species distributions and changes in resource use (Le Meillour et al., 2020). For example, cetaceans are morphologically hard to identify from traditional zooarchaeological analysis. ZooMS has become an alternative method for more accurate taxonomic identification of these specimens, which might otherwise not be identified (Kitchener et al., 2004; Speller et al., 2016; Rodrigues et al., 2018; van den Hurk et al., 2020, 2021; Wagner et al., 2020). Based on palaeoproteomic data, scientists were able to suggest an expanded distribution range for gray whales in the Mediterranean (Rodrigues et al., 2018), providing information that could be used to define ecological and evolutionary thresholds. When placed in an archeological and historical context, key aspects regarding cultural thresholds have been also explored, such as the dietary use of cetaceans for humans in the Roman and Medieval periods (van den Hurk et al., 2021), and by the American hunter-gatherer-fisher communities of Tierra del Fuego (Evans et al., 2016). Palaeoproteomics can be a stand-alone useful tool for marine areas where preservation of zooarchaeological remains are scarce—e.g., for remains in tropical and subtropical zones (Hofreiter et al., 2014; Speller et al., 2016)—as well as a supportive tool when integrated with other techniques (Evans et al., 2016; Rodrigues et al., 2018).

Determining Thresholds: Practical Limitations

The ancient biomolecular techniques discussed above are all established avenues of research for better understanding the human and beyond-human past. Yet, each of these techniques

is also subject to particular limitations that stem from working with damaged, degraded, and/or partial material. Access to paleontological and archeological materials from which these molecules can be extracted is also a constraint on ancient biomolecular research. As each of these techniques necessitates some form of destructive analysis, research must be carried out painstakingly to minimize the risk of wasteful destruction of unique paleontological and/or archeological materials. Each approach is further limited in scope by the availability of archeological and paleontological remains, which are often biased toward particular regions (terrestrial ecosystems and Europe in particular). There are ongoing efforts to expand these fields into less “traditional” regions of the world (for example, the ERC-funded 4-Oceans project), but this will continue to be limited by both differential preservation in different climates and by problems of access, including funding and training opportunities. Each of these biomolecular techniques additionally has an upper limit on the time depth to which they can be used. Thus far, the oldest ancient DNA ever retrieved was 1 million years old (van der Valk et al., 2021), but the majority of ancient DNA is significantly younger. Both stable isotopes and proteomics can go much further back in time, but are still limited by access to suitable remains for analysis. We here highlight additional limitations that must be considered for each of the proposed biomolecular approaches.

Ancient DNA

Ancient DNA, while providing a wealth of information, can be costly. Ancient DNA laboratory work requires access to specialized equipment and high-level clean lab protocols to minimize the risk of contamination by modern biomolecules. Ancient DNA has a high risk of contamination, therefore all laboratory work must be conducted by experts in specialized clean facilities for working with old, fragmented DNA. In the past, the sheer cost of conducting ancient DNA lab work (not to mention the associated costs and computational requirements for analysis) has been prohibitive for many labs. However, as high-throughput genomic sequencing has become more prevalent in molecular ecology, population genetics, and medicine, the associated cost of ancient DNA sequencing and analysis has been driven down in conjunction (Der Sarkissian et al., 2015). As a result, the number of ancient genomic sequences being produced has increased exponentially in recent years (Marciniak and Perry, 2017; Skoglund and Mathieson, 2018; Brunson and Reich, 2019). Recent advances in laboratory protocols and bioinformatic techniques have also reduced the impact of bias from post-mortem damage (Jónsson et al., 2013; Schubert et al., 2014; Prüfer, 2018) and expanded the capacity to conduct research on extremely poor-quality data (Ferrari et al., 2021a). The uncertainty associated with analyzing damaged DNA sequences can impact evolutionary analysis, but recent work on methodological development has done much to address this (Prüfer et al., 2010; Martiniano et al., 2020; Orlando et al., 2021). By using ancient DNA in conjunction with modern genomes, some of the limitations of ancient DNA can be addressed and ancient DNA can provide additional insight into deeper evolutionary history than modern genomes alone (for more

detailed discussion of ancient DNA applications and limitations, see Slatkin and Racimo, 2016; Pont et al., 2019; Spyrou et al., 2019; Dehasque et al., 2020; Smith A. D. et al., 2021).

Stable Isotopes

Stable isotope analysis of archeological material faces similar problems to the other biomolecular techniques. Sufficiently preserved material must be obtained and destructive analysis is required for collagen extraction (Hoke et al., 2018). The quality of stable isotope results can also be impacted by contamination (Vaiglova et al., 2014) and diagenetic processes that result in isotopic degradation, both of which have been addressed in recently published guidelines for quality-control stable isotope analysis (Guiry and Szpak, 2021). It can also be difficult to determine the comparability of environments across time. For example, whether differences in isotopic signatures across time are merely a reflection of chronology or actually indicate a significant change in environment or diet. This is an issue for $\delta^{15}\text{N}$ analysis, which is often used in marine ecology and historical ecology to conduct trophic web analysis (Jennings and van der Molen, 2015; Guiry, 2019). In order to account for chronological change, it is often necessary to find $\delta^{15}\text{N}$ values for a species that would have been close to the baseline of the trophic web both in the past and in the present to provide accurate trophic level estimation for the target species (Post, 2002). It is not always possible to access baseline trophic web species from past ecosystems, thereby limiting the power of trophic web analysis in the past. However, past dietary analysis using carbon and nitrogen signatures is an established and successful field in historical ecology and biomolecular archeology (Miller et al., 2020; Bird et al., 2021), as well as various other applications, including elucidating cultural thresholds in resource use (Lewis and Sealy, 2018; Nord and Billström, 2018; Miller et al., 2020) and geographic region of origin (Hobson, 1999; Lightfoot and O'Connell, 2016).

Palaeoproteomics

The advantages of palaeoproteomics include being putatively less destructive than stable isotopes and palaeogenomics, and that proteins can be extracted from very old material. However, proteomics and palaeoproteomics cannot provide as fine-scale information as ancient DNA, as it is not yet possible to conduct more than rudimentary evolutionary analysis such as phylogenetic assignment and taxonomic identification (Welker, 2018; Horn et al., 2019). Even if less dependent on material preservation, palaeoproteomics still relies on material quality and protein evolution. Poor recovery of peptides in ancient samples, as well as protein similarities between close-related taxa, can restrict palaeoproteomic studies to identification on higher taxonomic levels (Speller et al., 2016; Buckley, 2018). Existing palaeoproteomics databases also show a strong geographic bias, as research efforts have been concentrated at a small number of institutions in Europe (Welker, 2018). Despite this, recent advances in proteomics show promise for greatly expanding the evolutionary applicability of palaeoproteomics (e.g., Runge et al., 2021) and it will likely be an important field in the near future as more applications are explored.

THRESHOLDS AND RESOURCE MANAGEMENT

All of the above analytic capacities of ancient biomolecular research are crucial for understanding our past relationship with the marine environment. To establish future sustainable measures for marine resource exploitation, it is necessary to contextualize today's sustainability and conservation efforts with knowledge of the long-term relationships between humans and these ecosystems. The data currently available on human impact are typically collected on decades-long bases, and almost never predates the beginning of the twentieth century. As discussed above, there is strong evidence for industrial-scale marine resource extraction that occurred up to 1,000 years ago, at least in the North Atlantic context and likely elsewhere. This understanding is based on historical records and the analysis of archeological sites and remains. These initial research efforts provide a platform for understanding the human relationship with the sea going far back in time. They also provide context for emerging biomolecular techniques and novel applications. The above methodologies should, therefore, always be conducted with as much ecosystem-wide information as is possible, acknowledging the limitations of working with damaged and/or partial datasets. By exploring the past population dynamics of one species, it is possible to gain long-term information on balanced ecosystem dynamics. This will provide us with tools for avoiding the catastrophic threshold in our near future: the tipping point.

It is too often that thresholds identified for sustainable human exploitation fall under the category of the tipping point, pushing population dynamics to the point of collapse. For example, the commonly used notion of "maximum sustainable yield" in many modern fisheries sets catch limits on exploited species based on the amount of spawning stock biomass that can be sustainably removed from the population (Tsikliras and Froese, 2019). In practice, maximum sustainable yield does not take into account ecosystem dynamics and fluidity, rather it is based mainly on the population size of the focal species, allowing extraction up to the point of population collapse (McEvoy, 1986). In the same way, whaling regulative measures, such as the potential biological removal level defined by the U.S. Marine Mammal Protection act, and the Strike Limit Algorithm by the International Whaling Commission, are also based on the minimum population estimates of the stocks and their carrying capacity (Wade, 1998; Givens, 2000). Application of these and similar approaches have led to marine population collapses around the world due to the combined effects of overexploitation and climate change (Guénette and Gascuel, 2012).

The marine historical ecology approach provides ecosystem-based measures for the determination of "sustainable yield" by broadening the definition of the threshold, establishing a conceptual space for ecosystem change that occurs outside of, and prior to, the tipping point. Broadening thresholds allows quantification of population dynamics in focal species that lead to ecosystem perturbation, providing threshold indicators that signal impending population or ecosystem collapse rather

than driving the system to the breaking point (Duarte et al., 2020). It has been demonstrated that ecosystem complexity and controlled exploitation measures have overwhelmingly positive impacts on human and societal health, the marine environment, and the health of global fisheries (Hutchinson, 2008; Howarth et al., 2014).

By utilizing thresholds that act as boundaries for ecosystem dynamics rather than bringing the population to the tipping point each year, sustainable management measures are more likely to ensure the ecosystem remains stable. Further, FAO nations have pledged since 2003 to put in place ecosystem-based fisheries management (EBFM) practices in fisheries instead of devising policies that only apply to individual species, as was previously the case (FAO, 2003). In practice, EBFM has been difficult to implement due to the lack of consensus regarding issues of practical application and scale (Trochta et al., 2018), yet is demonstrably crucial to adapting to climate change (Holsman et al., 2020). The threshold concept provides a clear framework for identifying ecosystem, evolutionary, and cultural dynamics that can assist with developing EBFM practices. To effectively enact regulations such as ecosystem-based fisheries management, it is necessary to understand long-term ecosystem dynamics. To do so we must provide space for input from research that emphasizes long timescales and incorporates human society into our understanding of an “ecosystem,” a perspective that has long been held by many indigenous communities (Salomon et al., 2014 and references therein).

Case Study—Sea Otters in British Columbia

We here highlight the example of sea otter conservation management in British Columbia as a case study in how this research approach can be practically applied to policy. Sea otters (*Enhydra lutris*) are native to the Pacific coasts of North America and northern Asia (Kenyon, 1969). During the North American fur trade of the eighteenth and nineteenth centuries, sea otters were a prized trade item due to their dense, soft fur (Ravalli, 2009; Berg, 2019). By 1929, sea otters were extirpated in British Columbia (BC) (DFO, 2019), and there was near complete extinction of the species (Ravalli, 2009). Sea otters are a critical species for maintaining the kelp forest habitat that used to spread from BC to Baja California (Estes and Palmisano, 1974), a high-productivity environment that likely assisted human migration to the continent ~20,000 years ago (Erlandson et al., 2007). Sea otters consume invertebrates such as mussels and, most notably, sea urchins; grazing herbivores that can devastate kelp forests when left unchecked (Estes et al., 2016). In the absence of sea otters keeping the invertebrate population low, there have been two main effects. First, the kelp forest habitat along the North American coast has been threatened as a result of the trophic cascade initiated by extirpation of the sea otter (Szapak et al., 2013). Second, a large shellfish industry sprang up in British Columbia, Alaska, and the Pacific coast of the United States to take advantage of the increasing numbers of desirable food species, such as abalones and clams (Gamble, 2021).

In BC, there has been a campaign to reintroduce sea otters to the region in an effort to save kelp forests from devastation by sea urchins. Beginning in the 1960s and 1970s, this campaign has successfully reintroduced sea otters to various places along the coast of BC (DFO, 2019). A 2009 Department of Fisheries and Oceans (DFO) Canada report showed a population increase rate of 19% per year from 1977 to 1995, before slowing to a rate of 8.4% per year from 1995 to 2008, with associated patterns in range expansion (Nichol et al., 2009). With increasing population density and ongoing range expansion, BC sea otters have begun to impact shellfisheries in the region, as shellfish are a shared prey among humans and otters. While otters are not the only factor resulting in diminishing returns from shellfisheries (other factors such as pollution and climate change are crucial components as well), they have become a point of contention among fishers and indigenous communities (Gregr et al., 2020; Gamble, 2021).

Szapak et al. (2012) examined the isotopic signatures of otter remains on Haida Gwaii, an island near Vancouver Island with a long history of occupation (Salomon et al., 2014, 2018). They found that over the course of the last 12,000 years, the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of sea otters around the island indicated the otters consumed a diet of primarily benthic invertebrates rather than benthic fish. Contextualizing these results with historical and ethnographic work, Szpak et al. (2012) concluded that these isotopic signatures reflect the long-term management strategies indigenous communities practiced to keep the sea otter population low. This conclusion was supported by further research efforts in ethnography, archeology, ecology, and history (Salomon et al., 2014 and references therein; Stevenson et al., 2015) not to mention indigenous activism and participation in sea otter conservation efforts (Salomon et al., 2018).

Slade et al. (2021) further analyzed this pattern by showing that mussel size over the course of occupation on Haida Gwaii was consistent with low levels of predation by sea otters. They go on to argue that current conservation DFO efforts, which are based on estimations of environmental carrying capacity in an abstract world in which humans are not present, are actually increasing otter population density beyond what the environment would have experienced over the last 12,000 years, thereby causing reductions in invertebrate populations that are threatening shellfisheries (Gamble, 2021; Slade et al., 2021). Recent historical ecology work has shown that the coastal ecosystems of BC were intensively managed by indigenous communities (Salomon et al., 2014), including selective culling of sea otter populations. This ultimately led to a localized system of mosaic micro-environments in which areas near human settlements were comparable to today's sea urchin barrens and areas further away from humans were thick with kelp forests and sea otters, a pattern which is mirrored in research on sea otters and ecosystem stability today (Smith J. G. et al., 2021). While there were likely fluctuations in local environmental stability, the regional environment remained stable over the course of the late Holocene.

Sea otters are an animal of great importance to the indigenous communities of BC (Salomon et al., 2018). Under current DFO

regulations, indigenous communities are only allowed to take 500 sea otters from the total population (Salomon et al., 2018; Gamble, 2021). First Nations activists have argued recently that in order to provide balance between sea otters and people, and by extension invertebrates and kelp forests, they should be able to practice the traditional management techniques of the past, including increasing the amount of sea otters that can be removed from the ocean each year (Salomon et al., 2018). This is just one critical aspect of first nations' perspectives on resource management in the BC coastal region (Lee et al., 2019). The recent biomolecular archeology work cited above has strengthened the argument that sea otter management cannot be based purely on false assumptions of "pristine" environments that existed prior to humans.

We highlight this case study not to argue for or against a particular mode of sea otter conservation management, but to illustrate the utility of our research approach. Through the use of ancient biomolecules, archeology, history, and ethnography, research on sea otter management in BC has revealed key thresholds for sea otter management that can be directly applied through policy: thresholds in sea otter population density (*ecological*) and thresholds in sea otter hunting (*cultural*). This research has provided new evidence showing localized, mosaic management techniques that persisted over thousands of years, resulting in long-term ecological and cultural stability in the region that endured through the late Holocene. Further research in this area could incorporate more direct applications toward threshold identification, including using ancient DNA to model sea otter population sizes in the past, that could be directly applied to management strategies and inform sea otter conservation.

The authors would like to note that sea otter conservation is a controversial issue. This case study is merely meant to illustrate the applicability of the thresholds research approach. For more information on the issue of sea otter conservation in BC, please see articles published in *Hakai* magazine (such as Salomon et al., 2014, 2018; Gamble, 2021, and references therein, Gregor et al., 2020; Slade et al., 2021).

CONCLUSION

To effectively conduct research on changing marine ecosystems, common frameworks and terminology are required. For compelling communication between researchers, this framework must be flexible enough to encompass a myriad of different fields and scales, and requires a shift to incorporate humans and human society into our understanding of the environment. We have introduced a new theoretical language and a generalized approach that incorporates commonly used ecological ideas to address these issues. The thresholds theory is a way to conceptualize ecosystems and ecosystem change that is both flexible and scalable to the research questions being addressed, and lends itself well to practical applications.

We will never return to the oceans of old. It is not the aim of this research to provide pathways for doing so. Rather, it will likely be required to foster new ecosystems as we move forward

into the future (Alagona et al., 2012; Duarte et al., 2020), therefore it is crucial to understand what constitutes a balanced ecosystem, the issue of ecosystem complexity, and the role humans might play in these ecosystems. In addition to establishing regulation and oversight to provide future sustainable marine management, consideration must be given to long-term evolution that has occurred between people and marine environments around the globe, such as the interplay between indigenous communities and sea otters in BC during the late Holocene. Funding efforts for marine historical ecology should be directed toward archeology and population genomics analysis for the marine ecosystems on which people most directly depend, including a targeted effort to fund research occurring outside the traditional spheres of Europe and North America. To provide food security in a changing world, the species people depend on need to be understood from an evolutionary standpoint; how have they adapted to past climate change, anthropogenic exploitation, and different actors in their ecosystems? Are balanced ecosystem dynamics in a north Atlantic context the same as in a Pacific island context? What are the local boundaries management programs must navigate to ensure ecosystem balance? Through the thresholds framework, marine historical ecology is poised to answer these questions and provide crucial information for establishing sustainable marine ecosystems for future generations of humans and the species living with them.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

LA and MA wrote the manuscript with contributions from FF. All authors contributed to the development of the theory and revised, and accepted the manuscript.

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