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Forensics Meets Ecology – Environmental DNA Offers New Capabilities for Marine Ecosystem and Fisheries Research

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Climatic changes and anthropogenic pressures affect biodiversity and community composition. These biodiversity shifts are recognized in marine ecosystems, but the underlying processes are barely understood so far. Importantly, human well-being highly relies on oceanic services, which are affected by anthropogenic pressures. Here, we review how interdisciplinary research approaches, with the incorporation of eDNA (environmental DNA) analyses, can help increase the understanding of complex ecosystem processes and dynamics, and how they affect ecosystem services. We discuss marine conservation issues in the light of life cycle aspects and conclude that eDNA can improve our ecological knowledge in some instances, for example, in tracking migration patterns. We also illustrate and discuss the application of eDNA analysis within the context of population genetics, epigenetics, geochemistry and oceanography. Embedded into an interdisciplinary context, eDNA can be exploited by a huge variety of methodological techniques, and can resolve spatio-temporal patterns of diversity, species, or even populations within ecological, evolutionary, and management frameworks.

Keywords: environmental DNA, eDNA, fisheries management, marine conservation, population genetics, ecosystem functioning

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INTRODUCTION

Across the globe, biodiversity declines and extinction rates have accelerated over the last few decades due to climate change and anthropogenic influences (IPBES, 2019). More data about recent biodiversity change is needed to outline the underlying mechanism of these processes (IPBES, 2019). Ecological theory and modeling rely on this data for accurately predicting the future of ecosystem services. With the help of model predictions, stakeholders are able to minimize negative effects. Understanding how communities respond to environmental change is an important aspect of monitoring biodiversity.

Anthropogenic influences are one cause of biological diversity change (Halpern et al., 2008; McGill et al., 2015). Human activities heavily shape marine ecosystems with important consequences for human economies and health (McGill et al., 2015; Culhane et al., 2018). For example, coastal areas can provide a variety of ecosystem services such as flood prevention

(e.g., mangroves), food, maintaining water quality, furthering medical discoveries, and decreasing disease vulnerability (Worm et al., 2006; Bernstein and Ludwig, 2008; Mace et al., 2012). Between 1970 and 2007, marine fisheries declined by 38% globally and are projected to decline further (Worm et al., 2009; Hutchings et al., 2010). Human-facilitated carbon release is also causing unprecedented levels of ocean acidification (IPCC, 2014). To know how anthropogenic influences have affected the seascape biodiversity, constant and consistent monitoring is needed (Kavanaugh et al., 2016).

People are willing, more than ever before, to invest in the restoration of nature due to increasing awareness of biodiversity's benefits (IPBES, 2019). Especially in the marine environment, conservation is becoming more important due to increased fisheries and overfishing. But in the past, protection efforts rarely met the expected outcomes (McClanahan et al., 2006). More research is needed to understand complex ecosystem processes, such as in climatic influences (Cardinale et al., 2012), resource use efficiency (RUE) (Hodapp et al., 2019) or geochemical cycles. To evaluate the conservation success of protecting an area, often just a few key species are monitored (e.g., Edgar et al., 2014) due to limited financial issues. Monitoring changes in species composition and abundance within the context of the biotic community can help to evaluate the success of protection efforts.

In order to extend existing monitoring techniques with highly effective methods, identification of species with molecular methods find its way into monitoring approaches. Hebert et al. (2003) put forth DNA barcoding to identify unknown organism tissues down to species level. This turned out to be a useful tool because DNA barcoding identifies species as well as other methods do (Krishnamurthy and Francis, 2012). Traditionally, barcoding studies classify organisms into molecular operational taxonomic units (MOTUs/OTUs) (e.g., Creer et al., 2010). These MOTUs/OTUs group highly similar barcodes together, collapsing intraspecific sequence variations and estimating interspecific similarity. To assign these MOTUs/OTUs to a certain species, traditional taxonomic classification needs to be used. This integrative taxonomy is highly recommended for research in conservation issues (Krishnamurthy and Francis, 2012). When traditional species identification is challenging or not possible, barcoding can sustain the reliability of results. Notable taxonomic challenges include larval stages and cryptic species, which may be best identified genetically (Ball et al., 2005). Genetic approaches of species identification rely highly on robust databases. Since databases are large and not always well curated, sequence comparison can sometimes lead to ambiguous results. Databases, like BOLD (Barcode of Life[1]), using integrative taxonomy approaches to ensure robustness of their database. Molecular identification coupled with robust taxonomic identification is increasingly important for building accurate genetic databases. The decline in funding for taxonomy and decrease in specialized taxonomic identification skill makes barcoding a useful tool if properly curated databases can be used. Databases using integrative taxonomy are highly recommended to ensure an accurate assignment of sequence information to species.

[1] www.boldsystems.org

A new methodology, the analysis of environmental DNA (eDNA) can help to address gaps in our knowledge about biological community change (**Figure 1**). eDNA is characterized as a mixture of DNA shed (through skin, mucous, feces, etc.) by many organisms into the environment (soil, water, air) (Bohmann et al., 2014). eDNA can be used to target single species, like invasive or rare species (e.g., Wilcox et al., 2018), but also can be used to investigate whole community compositions when combined with metabarcoding approaches. Cost effectiveness, sensitivity, and non-invasiveness (e.g., Smart et al., 2015, 2016) are just a few benefits of eDNA approaches, helping to increase the understanding of biodiversity in a changing world.

Environmental DNA analysis can be used to target one or multiple species (**Figure 1**). In some cases, single species approaches using eDNA can be very beneficial, for example the use of qPCR for early detection of invasive species (see Section "Ecological Theory – An Overview"), or to estimate relative abundances of species (see Sections "Fisheries Management" and "Rare and Endangered Species"). If only a single species is pertinent to the interest of a study, some evidence suggests species-specific qPCR methods may be slightly more sensitive to detection than multi-species metabarcoding eDNA approaches (Harper et al., 2018; Bylemans et al., 2019). Environmental DNA metabarcoding, which is one of the most common techniques to detect species diversity, can be used to survey multiple taxa on both spatial and temporal scales for bioassessment (Taberlet et al., 2012, 2018; Stoeckle et al., 2017; Pawlowski et al., 2018). This technique uses PCR to amplify informative genetic targets using universal PCR primers, usually in commonly amplified mitochondrial, ribosomal, or nuclear regions. With eDNA metabarcoding, it is possible to identify multiple taxa, usually within a specific clade, such as fish or metazoans (Valentini et al., 2016; Ruppert et al., 2019). A similar approach is Tree of Life (ToL) metabarcoding where eDNA is shotgun sequenced to assess biodiversity at an holistic ecosystem level (Stat et al., 2017).

Dark diversity, biological diversity in an area which is not identified via traditional methods, may be obtained by eDNA methods (Boussarie et al., 2018; Cowart et al., 2018). This can help illuminate a fuller picture of a studied ecosystem. As well, eDNA can improve detection rates of poorly known and difficult to sample organisms (Wilcox et al., 2016). Using eDNA has the advantage of identifying species which are cryptic or taxonomically challenging to identify, e.g., larval stages, compared to more traditional methods such as nets and visual surveys (Thomsen et al., 2012b; Schmelzle and Kinziger, 2016; Yamamoto et al., 2017). Besides identifying an increased or more accurate list of taxa, eDNA can be used for monitoring changes in marine community composition. Already, eDNA has been used to document some community-level shifts in a variety of human-mediated environments (Pawlowski et al., 2014).

Since Ficetola et al. (2008) used eDNA to detect macrofaunal species presence, the use of eDNA has grown exponentially. With increasingly interdisciplinary research, we can see the power of combining singular techniques and methods to obtain a fuller picture of ecological patterns and processes. For example, combining observations of community change with geochemical

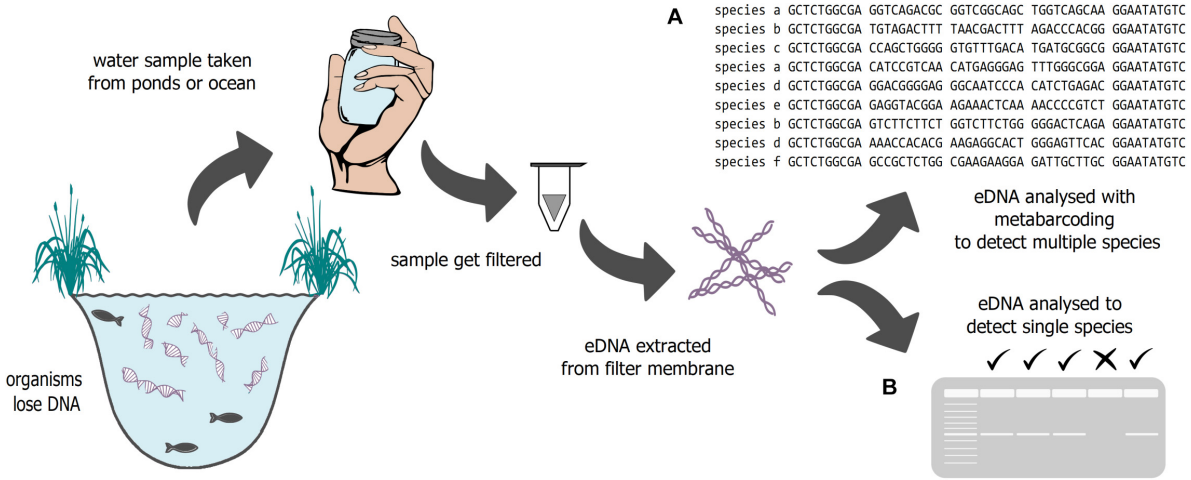

FIGURE 1 | Schematic illustration of eDNA sampling. DNA fragments are filtered out of water and extracted. The fragments can be analyzed either to investigate **(A)** community structure or **(B)** the presence or absence of certain species.

parameters (e.g., Osterholz et al., 2016) or combining species distribution patterns with hydrodynamics (e.g., Stuckas et al., 2017) has yielded information about how communities are changing. Environmental DNA analysis can also be used in other fields, not just to monitor biodiversity. Implementation of eDNA analysis, for example, in the field of population genetics or toxicology (Zhang, 2019), can offer a huge potential (Adams et al., 2019). The fusion of advanced technologies can result in highly promising tools, helping us save our oceans.

In this review, we focus on the implementation of eDNA-based approaches in an interdisciplinary context for marine management and conservation. We focus on eDNA studies in the marine environment, but also include some freshwater studies to give a broad overview of possible applications. Furthermore, we give an overview on current state of relevant ecological theories and their implementation into marine management and conservation. We do our best to include all relevant publications to displaying the state of these fields, but the rapidly expanding eDNA literature is not necessarily limited to just the cited studies. Here, we highlight studies where eDNA approaches were used in the context of marine monitoring. We also provide an outlook on future possibilities for improving interdisciplinary research approaches.

MARINE MANAGEMENT AND ECOSYSTEM FUNCTIONING

Ecological Theory – An Overview

Marine ecosystems are threatened more than ever from anthropogenic impacts. Increased fishing, environmental pollution, and human-driven climatic change accelerates extinction rates and biodiversity loss in our oceans and around the globe. Stable ecosystems can offer a huge variety of services for humans. The awareness of interrelations between ecosystem services, biodiversity and community composition in stabilizing ecosystems (**Figure 2**), rose over the last 30 years (Cardinale et al., 2012). The complexity of ecosystem processes requires the gathering of large datasets to understand these interactions. Some of these mechanisms have just recently been discovered, like for example the impact of RUE on a community level (Hodapp et al., 2019) or the stabilizing effect of far-ranging top predators on meta-food webs (Brechtel et al., 2019), and many may still be undocumented. The loss of biodiversity entails a decline in total biomass production (Hillebrand and Cardinale, 2010), which makes fisheries management essential for sustainable future ocean ecosystems. This section gives a simplified overview about the recent state of knowledge in ecosystem theory in relevance to this review.

The acceleration of climatic changes in the last century is one of the major drivers of biodiversity loss and the reduction of biomass production (IPCC, 2014). The use of fossil energy sources is the most critical anthropogenic driver (dark green arrows, **Figure 2**) of increased atmospheric CO_2 concentrations, beside deforestation (leading to decrease in CO_2 binding capacity). The increased atmospheric CO_2 concentrations (+ 40% since 1750) led to global temperature increase, in oceans + 0.11°C per decade (1970-2010) (IPCC, 2014).

This temperature increase can lead to intraspecific changes in physiology as, for instance, in juvenile hydroids (*Hydractinia echinata*) showed increased respiration rates of up to > 50% when exposed to + 3°C (Eder et al., 2018). Additionally, phenology can be affected by temperature increase. For example, plankton blooms (*Ceratium fusus*) shifted from September (1958-1980) toward July (1981-2002) (Edwards and Richardson, 2004), leading to interspecific phenological mismatches (e.g., Doney et al., 2012; Asch et al., 2019). Increased temperature can also force more frequent extreme weather events (storms, heavy rainfall, heat waves, etc.), which can alter phenology as well (e.g., Jentsch et al., 2009). Increased temperature has the potential to change biogeochemical cycles (Doney et al., 2012), the most famous example here is reduced growth of calcifying organisms,

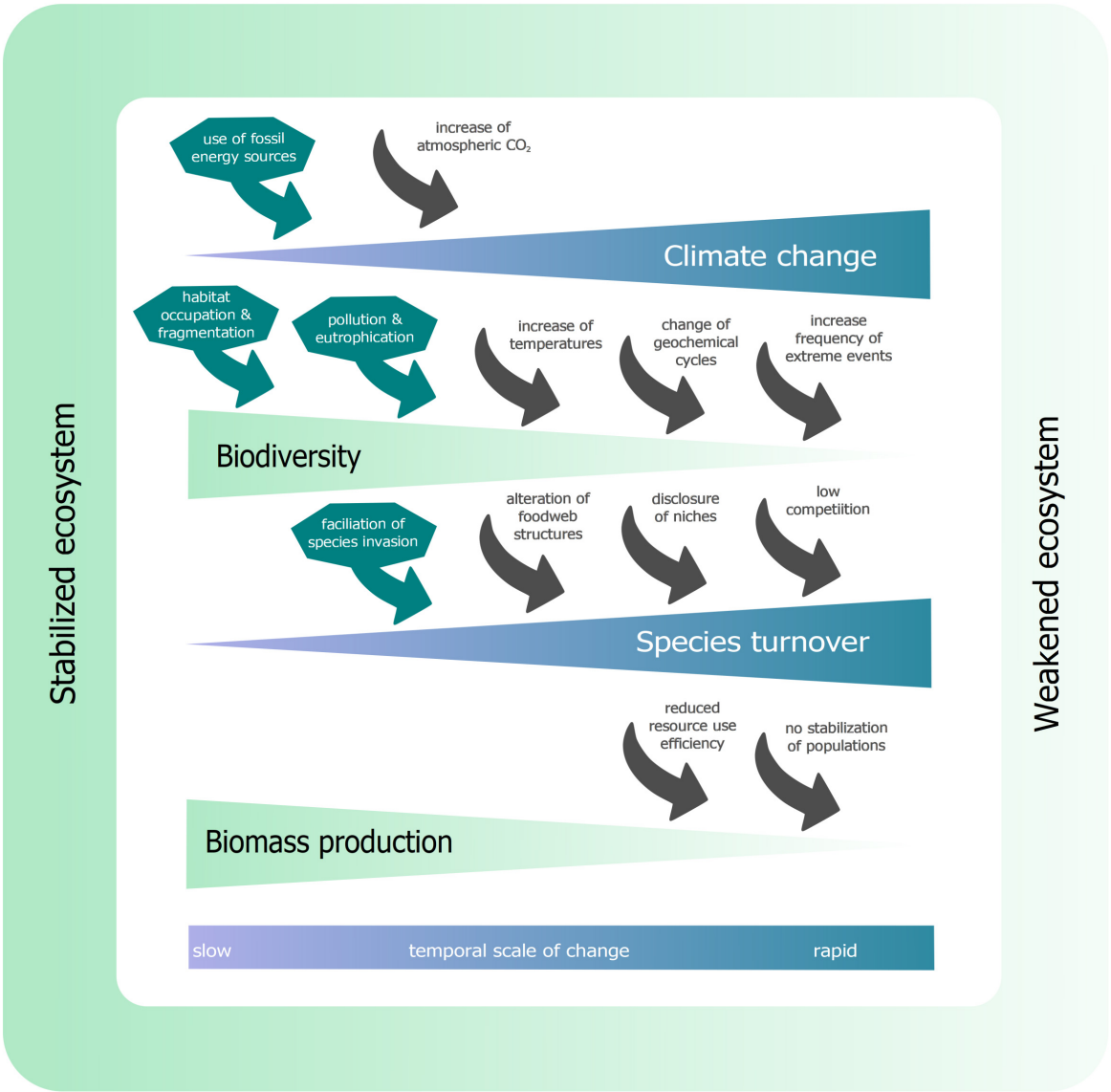

FIGURE 2 | Interactions between climate change, biodiversity and biomass production. Anthropogenic influence (dark green arrows) accelerates climate change, biodiversity loss and species turnover rates from outside the system. Within the ecosystem (gray arrows), changes in climatic conditions force biodiversity loss, which accelerates species turnover rates through the reduction of invasive resistance. These increased turnover rates lead to a reduced biomass production. This figure is a composition of various studies, modeling the effects within ecosystem dynamics, including meta-analysis studies (see Section "Ecological Theory – An Overview").

like diatoms or bivalves (Beaugrand et al., 2012). Additionally, geochemical cycles can be altered due to anthropogenic eutrophication (Howarth et al., 2011). All these drivers can affect species directly or indirectly, and reduce biodiversity in an ecosystem. In addition, anthropogenic drivers, like habitat conversion and occupation as well as environmental pollution, can force a loss of biodiversity.

Species can, due to environmental changes or by the opening of pathways, enter new biogeographical regions and establish an invasive population there. In an ecosystem with high biodiversity, the resistance to invasion is much higher (Kimbro et al., 2013). In an ecosystem with many different species, resources are efficiently used and it is hard for an invading species to compete with already established allocation of resources (Hodapp et al., 2019), in other words, filled niches. This is reinforced by rare species occupying small niches, which are, therefore, no longer available for invading species (Lyons and Schwartz, 2001). From anthropogenic activities, opportunistic species can get introduced into a foreign ecosystem, including new diseases and pathogens (Crowl et al., 2008). The loss of biodiversity can open previously filled niches and alter food web structure, which facilitates the invasion of species (Lyons et al., 2005). All this can accelerate species turnover rates. Ecosystems with high species turnover rates are likely to have a reduced resource

use efficiency (RUE) (Ptacnik et al., 2008). This and the new competitions from invasive species can make it hard for species to establish a stable population and optimize their RUE. This can result in a lower total biomass production (Ptacnik et al., 2008; Hodapp et al., 2019).

Not only can the presence or absence of certain species affect ecosystem dynamics, but this decline also reduces genetic diversity, which can lead to a reduced resilience or plasticity to changing environmental conditions. Therefore, species and populations would have a lower speciation potential (Brennan et al., 2019). Fewer individuals also increase the chances of inbreeding, which often negatively impacts populations (Charlesworth and Charlesworth, 1987; Charlesworth and Willis, 2009). The loss of genetic diversity can negatively impact ecological resilience during extreme events (Reusch et al., 2005). This general description across habitats may not apply to all ecosystems. Please note that the arrows shown in **Figure 2** are not the only possible connections in ecosystem functioning.

Fisheries Management

Oceans ecosystem services have been estimated to represent more than 60% of the global economic volume (Costanza et al., 1997; Martínez et al., 2007). Obtaining these socioeconomic benefits calls for ecosystem-based fisheries management. This strategy focuses on the health of the marine ecosystem as well as the fisheries (Pikitch et al., 2004). Monitoring changes in marine ecosystem dynamics can provide insights into the alteration of ecosystem functions. Therefore, a cost-effective monitoring method is needed. The analysis of eDNA can help achieve this (e.g., Jerde, 2019).

Traditional and Novel Monitoring

The past decades have given us a lot of insight into fisheries and the marine realm through the use of traditional sampling methodologies. Nonetheless, like every method, traditional methods have their limitations. For example, visual methods, like UVC (underwater visual census), BRUVS (baited remote underwater video station), diving, or snorkeling are very expensive due to high personnel costs. Additionally, diving methodology is restricted to accessible habitats with clearer waters. Other methods, like bottom trawls, fyke nets, multi-mesh gill nets, or other catching methods are invasive and can be destructive to habitat structures and species. For example, bottom trawling can destroy corals and effects are often long-lasting (e.g., Althaus et al., 2009). Therefore, invasive methods may not be the best choice for use in protected sites such as marine protected areas (MPAs). Behavioral aspects, like avoidance, can as well influence the precision of monitoring techniques (e.g., Boussarie et al., 2018). Environmental DNA methods further extend this range of traditional tools to explore and monitor fisheries.

Several studies investigated the effectiveness of eDNA-based methods compared to these established methods. For example, Thomsen et al. (2012a) compared eDNA metabarcoding with nine different traditional methods (angling, day- and night-snorkeling, beach seine, fyke nets, push nets, fish pots, multi-mesh gill net, bottom trawl) to observe a fish community. They were able to detect higher or equal fish diversity with eDNA analysis than with traditional methods. Several other studies also addressed how well eDNA reflects teleost diversity compared to traditional methods (e.g., Schmelzle and Kinziger, 2016; Valentini et al., 2016; Sigsgaard et al., 2017). Boussarie et al. (2018) were able to detect more shark species with the analysis of eDNA than with UVC and BRUVS. More broadly, Stat et al. (2017) were able to detect 287 families across the eukaryotic kingdom, showing the breadth of taxa detectable by eDNA analysis. Despite the benefits of effectiveness of eDNA-based methods, monitoring with traditional methods is worthwhile because allows long-term monitoring due to comparability of datasets and provide additional information, like age and sex of the individuals, that eDNA-based methods cannot provide. Moreover, the single methods shine a light on different aspects of a biological community (**Figure 3**).

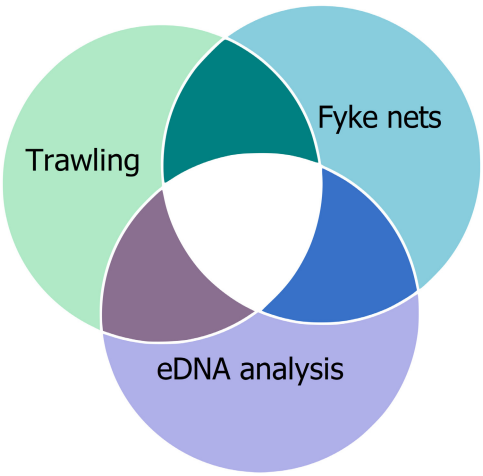

FIGURE 3 | Toward a more complete understanding of community composition. While results may overlap between monitoring techniques, no single method entirely captures species richness. We suggest combining multiple tools to obtain a more complete picture of biological diversity, as each method has its own strengths and weaknesses. For this example, trawling, fyke nets, and eDNA analysis would be used to capture biological diversity, however, these are not the only techniques available. Methodology should depend in which questions and taxonomic groups are of interest.

The involvement of fisheries records is highly beneficial for diversity monitoring and for the monitoring of key species. Conversely, ecological theories can help to improve fisheries management as well. This win-win situation has recently improved, as fishing activities were used to test ecological theories (Jensen et al., 2011). Evaluating fisheries data can give insights in influence of density depended spatial distribution of populations (reviewed in Jensen et al., 2011). For example, Merder et al. (2020) tested the density-dependent suppression of population biomass by using data from fish traps. This study verified the effectiveness of 'catch-and-wait' fisheries, where caught organisms were size-selected and small organisms were placed back into the environment. But fisheries data can also help to understand ecosystem dynamics and processes, like regime shifts (ecosystems abruptly shifting into another discrete state) or changes in trophic cascades (reviewed in Jensen et al., 2011).

Worm et al. (2006) compared catch data and ecological survey data and found an increased stability, i.e., higher recovery rates and lower collapsed fish/invertebrate stocks, in highly diverse ecosystems. These studies show that it is highly beneficial to use fisheries data as large ecosystem-scale experiments.

Stock Assessments

Nearly all traditional monitoring methods require significant sampling effort and personnel with high taxonomic expertise. Due to the continuous decline of taxonomic experts (Hopkins and Freckleton, 2002; Fischer, 2013), the probability of biases through misidentification increases. Taxonomic expertise is often highly specialized to a certain family or even genus due to its complexity. This specialized expertise may bias community richness results, skewing toward a particular genus, order, or family (Goodwin et al., 2017). When monitoring entire communities, identification via morphology requires high levels of expertise and time, which is often not feasible. Metabarcoding methods rely on complete and accurate libraries for environmental genetic assessment, so gaps in databases such as NCBI pose a challenge. However, as databases continue to improve, so will the detection of biological communities with eDNA. Here, we highlight some potential uses of eDNA should the databases be available for the species of interest.

A promising tool to assess fish stock sizes is the method of close kin-mark recapture (CKMR) (Bravington et al., 2016). With this pseudo-likelihood approach, it is possible to estimate stock size through fish kinship in a specific area or fishing ground. The more related caught individuals are, the smaller the stock is. CKMR is a recently developed method, combining evolutionary genetics with advanced mathematics (Bravington et al., 2016).

Fish stock assessments via catch per unit effort (CPUE) or occupancy modeling have been established for several years now and are widely used in marine management. Several studies investigated the potential of biomass/abundance estimation with correlation to the concentration of target eDNA fragments (e.g., Thomsen et al., 2016; Salter et al., 2019). Yates et al. (2019) recently conducted a meta-analysis with data from 19 studies and showed a weak correlation between eDNA concentration and abundance. In certain cases, it is possible to correlate the concentration of target eDNA fragments with the biomass of the respective target species (e.g., Lacoursiere-Roussel et al., 2016; Thomsen et al., 2016), making the implementation of CPUE in eDNA-based studies promising. Nonetheless further research is needed before eDNA concentrations can be reliably correlated to biomasses, since eDNA shedding and decay rates are highly variable between species and environmental conditions (e.g., Collins et al., 2018).

Models, such as occupancy models, try to translate scientific data into management-relevant estimations. These models estimate species occurrence and occupancy while accounting for possible non-detection or species misidentification (MacKenzie and Bailey, 2004). Site occupancy models can factor in non-detections, i.e., the patchy distribution of species. This makes site occupancy models a robust statistical framework for eDNA-based presence/absence studies (Schmidt et al., 2013). For example, Schmelzle and Kinziger (2016) compared eDNA-based detection of tidewater goby (*Eucyclogobius newberryi*) with a traditional method (multiple, paired seine hauls) by using multimethod occupancy modeling. They found that the detection probability using eDNA was nearly twice as high as for seining. They also found that eDNA concentration was positively correlated with CPUE (based on seine hauls) of tidewater goby (Schmelzle and Kinziger, 2016). This study shows, that eDNA analyses results can be applied in a wide range of established stock assessment frameworks.

Invasive Species

Marine management approaches also have to consider increased species invasions and their effects on ecosystem dynamics. The profound impact of biodiversity and ecosystem functions of invasive species has attracted the attention of management for over two decades (Pejchar and Mooney, 2009). The immigration of opportunistic species into a new habitat itself is a natural evolutionary process, a natural range expansion. But, due to human activities in marine ecosystems, this process has dramatically accelerated (Occhipinti-Ambrogi and Galil, 2010). The introduction of invasive species does not only have direct effects on community composition (see Section "Ecological Theory – An Overview"), e.g., through displacement of native species, but also on food web structures or even alter fundamental processes (ecosystem engineering species), such as nutrient cycling and sedimentation (reviewed in Molnar et al., 2008).

Ecosystem services can, as well, be impacted by the occurrence of non-native species, but in both, positive and negative ways (Katsanevakis et al., 2014). For example, the blue mussel, *Mytilus edulis*, is commercially important in human food provision. Due to the invasion of the Pacific oyster, Crassostrea gigas, into the southern North Sea, the biomass of blue mussels in this area decreased and the oysters changed the habitat structure (Kochmann et al., 2008), which had a negative effect on ecosystem services. However, the Pacific oyster is a commercially important species. This had positive effects on ecosystem services, because it offers a new economic sector. After some years, the ecosystem seemed to balance out and the blue mussel grew underneath the oyster-beds (Reise et al., 2017), benefiting from the oysters' protection against the main predator, *Carcinus maenas*, and biodiversity increased (Markert et al., 2009). Thus, an introduced species has the potential to increase diversity and total biomass production of the ecosystem (**Figure 2**), like in the example of the oyster-beds, diversity as well as total biomass production increased (Markert et al., 2009). The invasion of species can force more efficient resource use, and, therefore, a higher ecosystem productivity, but only if the species' traits fill a niche in the existing system (Hodapp et al., 2019). Nonetheless, invasive species more often have a negative impact on ecosystem functioning (Katsanevakis et al., 2014). If an introduced species competes with one or more native species in an ecosystem, it can decrease diversity and accelerate species turnover rates, which can lead to a decreased total biomass production (**Figure 2**).

The awareness of invasive species affecting ecosystems increases the need for fast, cost-effective, and standardized methods (Darling and Blum, 2007). DNA-based methods to identify species presence, within the context of species invasions,

especially in their early life stage, has proven to be highly suitable (e.g., Radulovici et al., 2009). In addition, the decline of taxonomic experts can narrow the scope to certain taxa (Taylor and Harris, 2012), and, thus, might lead to a misinterpretation of invaders and their impact on ecosystem dynamics.

Using molecular methods, the presence of species can be detected solely through their DNA traces in the environment. With the analysis of eDNA, it is possible to track the spatial and temporal occurrence of species (e.g., O'Donnell et al., 2017). The incredible sensitivity of this method allows the detection of only a few individuals entering a new area (e.g., Ardura and Zaiko, 2018). For example, Marshall and Stepien (2019) were able to detect the invasive Eurasian zebra and quagga mussels (*Dreissena polymorpha* and *D. rostriformis*) across all life stages. As well, eDNA results delineated species compositions, and even population-level diversity (see Section "eDNA and Evolution") differences among ecosystems (Marshall and Stepien, 2019). Studies investigating the spatial distribution of aquatic animals has been done for a variety of taxa (e.g., red fin perch; Bylemans et al., 2016). Defining spatial resolution of species distribution in marine systems are, to our knowledge, not proven, due to the lack of knowledge about water body movements and the degradation characteristics influencing the spread of eDNA (see Sections "eDNA and Water Chemistry" and "eDNA and Hydrodynamics").

Pathways of Introduction

Since the removal of an already established invasive species is usually unsuccessful (Thresher and Kuris, 2004), monitoring and regulation of introduction pathways can prevent species invasion (Molnar et al., 2008). Opportunistic species can enter new habitats in a variety of ways. Some of the major pathways are unbarred via globalization and increased transport across the world, for example, larval transport via ballast water or organismal transport through hull fouling (Molnar et al., 2008). One of the challenges of ballast water monitoring is that many of these invasive species may be in larval form, which makes them difficult to identify morphologically (McManus and Katz, 2009). This is especially important to consider in light of declining taxonomic expertise (Hopkins and Freckleton, 2002). Species identification via metabarcoding with well-curated databases can be implemented by monitoring ballast waters with eDNA to improve the effectiveness of invasion prevention.

Some of the first studies to metabarcode eDNA/bulk samples from ballast water used universal CO1 and RuBisCo markers from a ship traveling from Germany to South Africa (Ardura et al., 2015; Zaiko et al., 2015a,b). Multiple taxa were identified to assess the biological communities traveling in ballast water ecosystems, including algal and mollusk species which can pose an invasion risk (Ardura et al., 2015; Zaiko et al., 2015a). Other studies have also used eDNA methods to detect Quagga (*Dreissena bugensis*) and Zebra mussel (*D. polymorpha*), but found that light transmission spectroscopy was more effective for detection (Egan et al., 2015). While eDNA methods alone may not be ready to become the only test for industrial-scale usage, these genetic methods of presence identification are likely to be a good complement to current methods (Zaiko et al., 2015b). This may especially be true if eDNA metabarcoding proves to be economical, fast, and can be standardized across labs.

Anthropogenic habitat engineering can also open the floodgates for species invasion. One of the most famous examples was the construction of the Suez channel that connects the Red Sea and the Eastern Mediterranean Sea in 1896. With this direct connection between the Indian Ocean and the Mediterranean Sea, more than 300 species migrated to new locations (Por, 1971; Bentur et al., 2008). This rapid breakdown of distribution barriers and the resulting acceleration of species turnover issued a challenge for ecosystem stability (**Figure 2**).

Another opportunity for species invasions is via aquaculture and fish farms, especially when species are cultured in an area in which they are not native. A recent example is the invasion of the Pacific oyster (*Crassostrea gigas*) into the North Sea. Due to increased winter temperatures, induced by climate change, escaped oyster larvae from the farming grounds established invasive populations (Diederich et al., 2004). This example also shows that anthropogenically driven species invasion has more than one facet that needs to be considered (here, climate change and aquaculture). But not only aquaculture needs scrutiny; nearly all occasions where living animals are transported comprise a high potential to open pathways for invasive species, like the trade of live seafood or the introduction of exotic pets (e.g., the aquarium trade) (Molnar et al., 2008).

How species enter new habitats is one of the most crucial areas for marine management. Geographically, pathways of invasion can be reconstructed via population genetics (Estoup and Guillemaud, 2010). For example, Hänfling et al. (2002) found that the Chinese mitten crab (*Eriocheir sinensis*) population, invaded in San Francisco, CA, United States, was founded by a single invasion event from European, not Chinese, populations by analyzing population genetic data. Increasingly, evidence has built up around eDNA population genetic studies (see Section "eDNA and Evolution") for improving our understanding of invasion pathways.

MARINE CONSERVATION

The conservation of biodiversity in highly endangered marine habitats is crucial due to high extinction rates (IPBES, 2019). In marine management approaches, stakeholders try to regulate the occurrence of certain species (e.g., invasive species), or the size and structure of stocks. Marine conservation approaches, by contrast, rely on the paucity of human influence, allowing nature to restore itself without much active management. A detailed knowledge about the spatial and temporal distribution of marine species is necessary for successful conservation.

Marine Protected Areas

Areas which are protected from most anthropogenic impacts, allow ecosystems to recover and stabilize. Modern protected areas were set up during the last 200 years in all habitats, but there is evidence that the ideas for protected areas are roughly 2000 years old (Phillips, 2004). In the 1970s, the establishment of protected areas increased exponentially, trying to restore biodiversity

and maintain ecosystem services, especially in marine systems (marine protected areas, MPAs). Positive effects of MPAs on socioeconomic value has been widely reported (e.g., McClanahan et al., 2006).

Monitoring biodiversity in MPAs and the surrounding area is one of the cornerstones used to evaluate the success of protection effort. So far, the abundance of some key species was estimated with traditional, mostly invasive methods, such as trawling. These invasive methods can impact rare or endangered species. The use of eDNA to evaluate diversity, or the occurrence of single species, can improve non-destructive monitoring in MPAs. But traditional, mostly invasive methods provide information that eDNA analysis cannot. For instance, size and gender of single individuals allows researchers to estimate the structure and health of a stock. Nonetheless, eDNA metabarcoding reveals great benefits, like the identification of rare species with lower sampling effort, potential abundance estimations, and species composition.

Rare and Endangered Species

The occurrence of rare species is one of the major criteria for the establishment of marine protected areas (MPAs). Another one is high diversity, so called diversity hotspots. Most of the time, rare species occur less often in areas where diversity is high (Prendergast et al., 1993). Naeem (1998) already proposed that rare species should have a large impact stabilizing ecosystem functions, based on ecological and engineering theories. Recent studies supporting this theory, like Mouillot et al. (2013), found that 98% of locally and regionally rare fish species highly support ecosystem function in coral reef systems. The maintenance of ecosystem functioning not only relies on high diversity, but on species-specific contributions to certain functions. Studies showed, for example, that the removal of rare species decreases the invasion resistance of an ecosystem (**Figure 2**; Lyons and Schwartz, 2001). The more rare species go extinct, the higher acceleration of species turnover will be.

The incredible sensitivity of eDNA analyses are not only beneficial to detect invasive species at an early stage, but also rare and endangered species that can easily and non-invasively be monitored. For example, Parsons et al. (2018) was able to characterize the stock structure of the elusive harbor porpoise (*Phocoena phocoena*) from inland waters of southeast Alaska. Beyond species presence, eDNA can identify the effects of invasive species on the distribution of native species (Wilcox et al., 2018), or even the distribution of invasive species itself and the efficiency of management efforts (Robinson et al., 2019).

Some studies indicate that eDNA-read abundance correlates either with the biomass or with the number of individuals (e.g., Salter et al., 2019). One of the first studies in the marine environment to correlate eDNA-read abundances with fish abundance, caught by trawling, was conducted in Greenland waters (Thomsen et al., 2016). However, the results were more nuanced. Some species had a more significant correlation between read abundance and trawl abundance than other species. This could be because many factors influence detectability and read abundance in an eDNA sample. This includes different shedding rates, according to life cycle stage, or different persistence rates, due to environmental conditions. Additionally, low density species may be detected stochastically depending on sampling effort, as is the case with all detection methods. How samples are obtained and preserved can interfere with certain lab procedure steps, thus, affecting detectability and read abundances (Mauvisseau et al., 2019). Different lab procedures, like extraction protocols or preservation, but also primer biases can cause variation in read abundances (e.g., Kelly et al., 2019). Biologically, eDNA shedding and persistence rates are highly species and life cycle specific (Sassoubre et al., 2016; Ahern et al., 2018). For example, higher biomass caused higher shedding rates of eDNA from Japanese jack mackerels (*Trachurus japonicus*) in a tank experiment (Jo et al., 2019). Thus, part of the difficulty in relating abundance to eDNA is that species-specific relationships will need to be teased apart.

Such discrepancies require a lot of preliminary work to evaluate accuracy when using a single species approach. Another possibility is the relative quantification of a species within the community (e.g., Valentini et al., 2016). The emerging growing technologies in the field of high throughput sequencing allows us to describe whole communities in one sequencing run (see Section "Pathways of Introduction").

However, eDNA is not currently used for providing concrete estimates of abundance, such as biomass or individual count (Hansen et al., 2018; Yates et al., 2019). To link eDNA to abundance in a marine environment, more studies need to be done to accurately model how eDNA moves through the water column. While this has been done for freshwater environments, the marine system presents more complex challenges, for example, tides and currents must be taken into account (Kelly et al., 2018; Lacoursiere-Roussel et al., 2018; Andruszkiewicz et al., 2019; Levi et al., 2019). In addition, eDNA cannot yet provide information like fish size and age, or gage hormone levels (Hansen et al., 2018).

Over time and increased research, eDNA may be able to provide information on species shifts and changes in species presence. With further developments, eDNA may become a tool useful for monitoring, more than simply detecting the presence of important species. Although fisheries research can start to harness eDNA to monitor species presence now (Thomsen et al., 2016), challenges relating to abundance and life-history descriptions need to be overcome to fully use eDNA for fisheries management.

Lifecycle Aspects

Over the past few decades, the implementation of animal behavior research into conservation considerations has improved the understanding of anthropogenic impacts on biodiversity. An organism's adaption to stressors, including anthropogenic stressors, is based on evolutionary processes, altering species behavior which might even affecting community composition (reviewed in Berger-Tal et al., 2011). The habitat alteration of spawning grounds, for example, can cause a spatial shift or a decline of species abundance; both can lead to local community shifts across trophic levels. Gosset et al. (2006), found that population size was significantly negatively affected by anthropogenic actions, due to the alteration of migration behavior. Annual or seasonal movement of marine species is

often triggered by at least one of the following reasons: mating, food availability, or climatic aspects (Lascelles et al., 2014). Additionally, life stages can force migration behavior. Juvenile or larval stage of marine species are often part of the zooplankton community. In this case, migration often takes place on a daily cycle. Berry et al. (2019) was able to identify 245 families of eukaryotic zooplankton with eDNA metabarcoding and the majority of them were at a larval stage. Another example is the vertical migration of Antarctic krill (*Euphausia superba*) known for nocturnal migration to feed on plankton at surface waters and diurnal migration to deeper waters for predator avoidance (Croxall et al., 1985). Relating to this vertical migration of krill, fish stocks follow this migration pattern to feed on (Kaartvedt et al., 1996). Life cycle migration in the Pacific Salmon (*Oncorhynchus* spp.) was detected with an eDNA analysis in a time series in AK, United States (Levi et al., 2019). Recently, conservation approaches tried to include such spatial variation due to life cycle stages, to improve the protection of endangered species (see Section "Implications for Marine Conservation"). Recognition of food web and life cycle migration aspects is a critical point to ensure successful conservation and eDNA analysis also be applied here.

Implications for Marine Conservation

Twenty-one percent of marine migrating species are considered to be threatened (Lascelles et al., 2014). Therefore, efficient monitoring of species diversity and richness in MPAs are highly useful to evaluate the success of protection. eDNA-based analysis can help to improve monitoring in this area, especially for rare and endangered species. However, migration patterns needed to be considered. Behavior-based modeling of spatial distribution and habitat use improves conservation success and should be one of the key tools for marine conservation (Norris, 2004). In recent years, the idea of pop-up protected areas has emerged (Runge et al., 2015). Knowledge about migration routes and times allow for protecting certain areas at that time, such as when endangered species migrate through (Runge et al., 2015). This terrestrial approach is highly promising for conservation and meets economic needs. We suggest this concept be used in marine conservation as well (**Figure 4**).

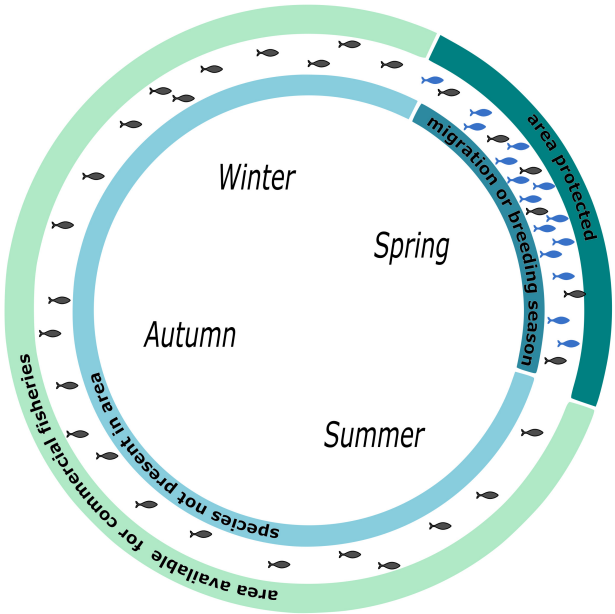

FIGURE 4 | Schematic illustration of pop-up protection areas in marine realm. Differential usage of a seascape by fisheries and conservation efforts. During the breeding season, the area is protected from fishing. Other times of the year, the area is open for fishing. Alternatively, a seascape could be protected during a migratory season.

ANTHROPOGENIC INFLUENCES ON MARINE COMMUNITIES

More broadly than fisheries decline, there is a need to monitor changes in the biodiversity of communities as they impact ecosystem services (Hooper et al., 2005) (see Section "Marine Management and Ecosystem Functioning," **Figure 2**). Community composition can be described with a variety of indices (Simpson, 1949; Pielou, 1966; Hill, 1973; Lande, 1996), traits (Litchman and Klausmeier, 2008; Weithoff and Beisner, 2019), and phylogenetics (Mouquet et al., 2012; Tucker et al., 2017) to predict how changes in community assembly over space and time may affect ecosystem function. To inform these models, individuals were captured through a variety of traditional methods such as nets (Siegenthaler et al., 2019), video (Stat et al., 2019), transects (Uthicke et al., 2018), and quadrats (Currier et al., 2018). However, because of the aforementioned decline in taxonomic expertise and effort of collecting samples (Hopkins and Freckleton, 2002), eDNA analyses, especially eDNA metabarcoding, are emerging as a genetic method for data acquisition to complement traditional sampling and can foster large scale community monitoring.

Aquaculture and Seascape Shifts

Seafood production through aquaculture and fish farms more than doubled since the 1980s (Asche and Smith, 2018). At least since the 1980s, fish farm impacts on the surrounding ecosystem have been well documented (Brown et al., 1987). These biological changes can now be quantified using eDNA-based methods as well as traditional methods (e.g., Stoeck et al., 2018a). One instance examined foraminiferal biodiversity using protist eDNA metabarcoding primers in areas both close and far from salmon farms in Scotland (Pawlowski et al., 2014). Samples farther from salmon nets showed greater species richness of foraminiferal communities compared to samples closer to salmon farms (Pawlowski et al., 2014). Other Scottish and New Zealand biodiversity investigations found similar results with bulk sampling for bacteria and protists (Dowle et al., 2015; Pochon et al., 2015; Stoeck et al., 2018a,b). New Zealand's Chinook salmon farms (*Oncorhynchus tshawytscha*) also showed that high waterflow sites had higher foraminiferal diversity than low waterflow sites, perhaps indicating higher water flow is better for the fish farm ecosystem (Dowle et al., 2015; Pochon et al., 2015). In British Columbia, foraminiferal alpha

diversity was lower close to salmon cages compared to more distant reference sites, though beta diversity showed impacts may differ between farms (He et al., 2019). Importantly, shifts in foraminiferal communities were investigated with both eDNA and eRNA, the latter providing a more recent snapshot of the community at large (Dowle et al., 2015; Pochon et al., 2015). The use of eRNA provides a better proxy for modern communities due to eRNA's shorter half-life in an environmental setting.

These impacts on biodiversity and community composition at the base of marine food webs are likely to be transferred through all trophic levels (**Figure 2**). Environmental DNA may persist for a longer period of time when using sediment as the environmental substrate (Turner et al., 2015), giving the opportunity to track community shifts over time (Armbrecht et al., 2019). Occurrence of phenological mismatches are one major driver accelerating species turnover rates (**Figure 2**). This, in turn, may decrease biodiversity as well as ecosystem biomass production.

Environmental Pollution Events

Not only salmon farms may shift surrounding community composition. Oil and gas operations also showed differing benthic community compositions when compared with reference sites (Laroche et al., 2018; Cordier et al., 2019). While all these interactions have been documented with other methods (Kalantzi and Karakassis, 2006), eDNA is an effective environmental impact monitoring tool for community biodiversity, especially for harder to sample meiofauna (Olsgard et al., 1998; Lejzerowicz et al., 2015; Stoeck et al., 2018b). eDNA has also been proposed to monitor mining areas, especially deep-sea mining, although this has yet to be extensively researched (Fernandes et al., 2018; Billett et al., 2019). More research is needed to apply this framework to bigger, free-swimming macrofaunal assessments. Their genetic signatures may not be as strong given the larger home ranges of many macrofaunal marine taxa (Boerder et al., 2019).

Environmental DNA can also be applied to monitor the aftermath of unexpected events, such as oil spills. After such events, eDNA can aid in quantifying the effectiveness of clean-up efforts to characterize ecosystem resilience and health (Ellis et al., 2012). For example, after the Hebei Spirit oil spill, eDNA monitoring was used to determine how well the micro- and meso-organismal communities bounced back (Xie et al., 2018). Immediately following the oil spill, bacteria which degraded hydrocarbon and algal families were stimulated by oily sediments, while protist communities changed (Xie et al., 2018). After five years, metazoan communities with less contaminated sediments started shifting toward diversity profiles similar to reference sites (Xie et al., 2018). Another example showed a shift in communities before and after the Deepwater Horizon oil spill (Bik et al., 2012). Before the spill, a high diversity of metazoans was present and DNA-based diversity was dominated by nematodes (Bik et al., 2012). In contrast, after the spill, fewer metazoan taxa were recovered from DNA reads and diversity was dominated by fungal reads (Bik et al., 2012).

By using eDNA metabarcoding to monitor meiofaunal communities, it is possible to quickly gain a sketch of how these events shift biological communities. In the future, eDNA methods may become more widely applied to a variety of these unexpected but community-shifting events, such as marine algal blooms or extreme environmental events (Dhar et al., 2015). For example, hurricanes can reduce coral cover by an average of 17% a year (Gardner et al., 2005). Marine heatwaves may also cause shifts in community composition (Berry et al., 2019). Such extreme environmental events are happening with greater frequency due to shifting climate (IPCC, 2014). Beyond the immediate monitoring of after effects, if areas of interest – commercial, recreational, conservation, or otherwise – are consistently monitored, then long-term datasets can start to be built and long-term patterns may emerge (Berry et al., 2019). From recognizing natural recovery patterns, management of these areas post-impact could potentially hasten or direct recovery.

Water Quality Assessments With eDNA

Anthropogenic activities beyond large events, such as oil spills, often lead to a change in chemical composition of aquatic environments. This starts with the discharge of nutrients leading to increased eutrophication of coastal areas (e.g., Rabalais, 2002), which in turn changes primary production and species composition (**Figure 2**). Graham et al. (2019) used a Bayesian network modeling approach to evaluate water quality in estuaries and describe community structure. Another approach elucidated the functional ecology of groundwater fauna, using eDNA-based community analysis as well as eDNA stomach content analysis (Sacco et al., 2019). The understanding of groundwater ecology and the shifts in community composition and functioning it can detect, is highly important for human well-being under the light of preserving water supply.

In ecotoxicological research, eDNA approaches can be implemented (Zhang, 2019). For example, the release of endocrine disrupting chemicals can facilitate phenological shifts, which may impact whole ecosystems (e.g., Segner et al., 2003) community response to toxic substances can be evaluated. Biodiversity changes caused by pollutants may affect ecosystem dynamics (Zhang, 2019). Single-species abundance changes may also be targeted with qPCR and specific probes. Thus, monitoring with eDNA-based techniques, whether it be metabarcoding for community or targeting a single species, can aid in discerning patterns of community-level shifts in ecotoxicological research and can inform management efforts.

INTERDISCIPLINARY FUTURE OF eDNA MONITORING

Currently, eDNA analysis can confidently detect species presence and describe species composition. The use of eDNA-based methods has many advantages, but the methods still require more research to overcome challenges and expand the scope of its use (Goodwin et al., 2017; Cristescu, 2019). We consider harnessing the wide potential of eDNA as a tool to answer evolutionary and ecological questions beyond presence and abundance by linking eDNA with other existing areas of research (**Figure 5**). One area would be to fully develop eDNA for discerning evolutionary

change, including for population genetic and epigenetic markers (Zhao et al., 2018; Adams et al., 2019; Sigsgaard et al., 2020). Other avenues may include adding eDNA to suites of ecosystem monitoring tools, such as combining eDNA with water chemistry to obtain a more complete idea of how abiotic and biotic factors are connected within an ecosystem over time and space (He et al., 2019; Zhang, 2019). Already, eRNA has been used in conjunction with eDNA to snapshot biodiversity at shorter time scales, and potentially to understand the biological processes present (Pochon et al., 2017; Zaiko et al., 2018; Cristescu, 2019). Lastly, we briefly touch upon the potential of combining hydrodynamics with eDNA methods and the increased interest of monitoring eDNA autonomously or by remote sensing methods (Scholin, 2010). Automation may aid in consistency of monitoring and reproducibility of research (Dunn et al., 1993; Pomati et al., 2011). While fine-tuning eDNA remains for ecological questions, eDNA shows flexibility and promise as a tool for ecosystem monitoring when coupled with other methods.

eDNA and Evolution

Population-Level Variation With eDNA

Modern eDNA analysis is increasingly being explored for genetic monitoring. Currently, groundwork is being laid for using eDNA to describe population genetic variation, mostly in marine environments (Adams et al., 2019). Recent work has focused on the ability to quantify haplotype ratios for quagga and zebra mussels (Marshall and Stepien, 2019). From aquarium and field experiments, there was a significant relationship between observed and expected haplotype ratios (Marshall and Stepien, 2019). This finding holds promise for using eDNA for both the ability to confirm existing phylogenetic relationships, discovering new haplotypic variation, and quantify this variation. However, more tests using other ecosystems and species will be needed to confirm this trend, but given the recent success, eDNA for detecting population-level variation may be on the horizon.

To be able to use eDNA for population genetic questions will require more research. First, some population genetic theory cannot be tested with eDNA if individuals cannot be identified (Adams et al., 2019). Many arguments for eDNA population genetic usage reflect that of pooled sequencing (poolseq), however, it is difficult to ensure that plentiful and equal amounts of individuals per species are in an eDNA sample (Schlötterer et al., 2014). To understand how haplotypes are distributed in a marine water column, the "ecology" of eDNA (see Section "eDNA and Water Chemistry") needs to be investigated. With this knowledge, genetic variation based on population-level diversity could be investigated for more marine species (Barnes and Turner, 2016; Marshall and Stepien, 2019). While evidence suggests correlation between eDNA population-level genetic variation and traditionally sampled genetic variation, this remains to be tested under other conditions (Marshall and Stepien, 2019). It is likely that bioinformatic filtering parameters may need to be system-specific and fine-tuned for eDNA population genetic research, rather than a one-size-fits-all approach (Alberdi et al., 2018; Turon et al., 2019). Furthermore, as a majority of eDNA population genetic studies have focused on mtDNA, if nuclear variation cannot be obtained, eDNA population-level variation may not be as informative as traditional genetic sampling (Elbrecht et al., 2018; Parsons et al., 2018; Adams et al., 2019). If population genetic eDNA technique is further developed, this can potentially open up the monitoring of within-species genetic diversity for multiple species at the same time (Stat et al., 2017; Elbrecht et al., 2018).

Epigenetic eDNA

Advantages of epigenetic eDNA – What is it and why do it

The integration of epigenetics and eDNA has the potential to allow researchers to quantify genetic variation in eDNA samples, and, thus, make use of basic population genetic frameworks (Zhao et al., 2018; Sigsgaard et al., 2020). Epigenetics, modifications of DNA which are not alterations to the DNA sequence itself, acts as an interface between the environment and genetics because modifications are made in response to the environment. While epigenetic variation such as methylation has yet to be extracted from eDNA sources, this presents an intriguing opportunity because information not normally obtained from eDNA could be detected. Heritable epigenetic changes could be used as measures of relatedness at a population level for distinguishing and comparing populations or individuals (Fraser et al., 2012; Zhao et al., 2018) and even individuals (Fraga et al., 2005).

Additionally, epigenetics reveal aspects of populations that eDNA genetic analyses alone cannot currently discern (Fraga et al., 2005). Methylation patterns differ with age and sex, which could be of interest for tracking population dynamics. Evidence also exists for different methylation patterns based on environmental factors, such as nutrition, temperature, and toxins (Gokhman et al., 2017). Epigenetics may also play a role in disease and pathogen resistance (Feinberg, 2018). Through obtaining epigenetic information, these environmental effects on target species could be determined. Moreover, due to the role of methylation in transcription, differences in gene expression between populations could be examined (Nätt et al., 2012). Variable expression from epigenetic markers could affect how organisms are locally adapted or hint as to what traits may be caused by phenotypic plasticity (Sahu et al., 2013; Aller et al., 2018; Yang and Andrew Pospisilik, 2019). Because eDNA is a bulk sample, epigenetic information for multiple species could be obtained from the same sampling event. Over time, ecological and evolutionary patterns may emerge at the community level. However, much more research, including proof-of-concept work, would need to substantiate any of these ideas before epigenetic eDNA (epi-eDNA) can be used for monitoring.

Epigenetic eDNA (epi-eDNA) challenges and how to address them

While analyses of both epigenetics and eDNA are powerful in their own right, epi-eDNA analysis likely faces multiple challenges before the approach can be routine and practical for in-field use. One challenge would be to separate out patterns of methylation, as different tissue types contain different patterns of epigenetic variation, even within the same

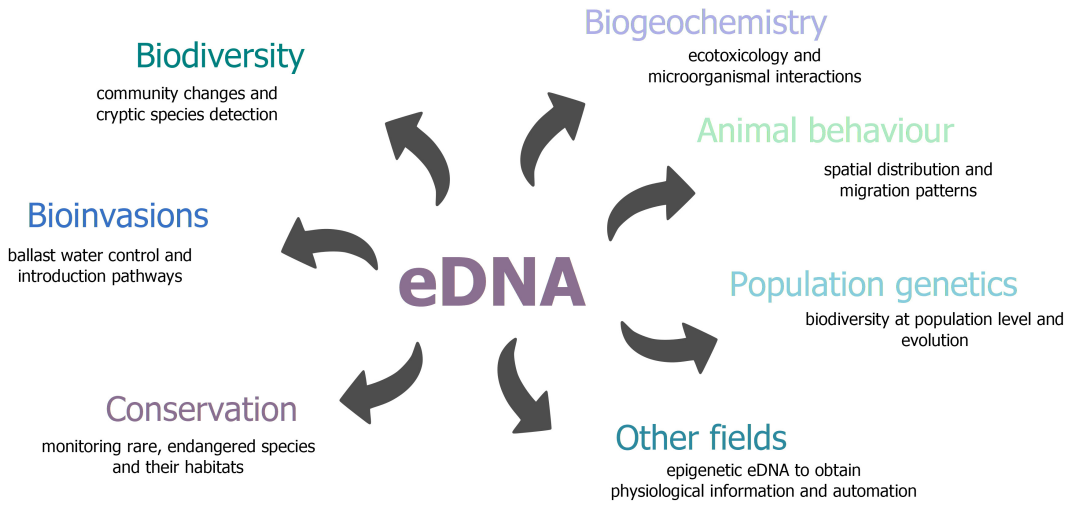

FIGURE 5 | Overview of research fields that can benefit from eDNA-based approaches. Outlined are a few potential applications.

individual (Christensen et al., 2009). Metastable epialleles, loci that are differently methylated between individuals but have low variability within the same individual, could be targets of epi-eDNA (Rakyan et al., 2002). This would require methylation maps across different tissues and individuals, which is not currently very common for non-model species.

Beyond finding a suitable target, epigenetic eDNA techniques would likely require well-preserved epi-eDNA, which may present technical challenges. However, isolating DNA from degraded sources such as ancient DNA is possible and has been done using bisulfate sequencing (Smith and Ryckman, 2015; Gokhman et al., 2016, 2017; Zhenilo et al., 2016). Alternatives to harsh bisulfate sequencing using enzymatic deamination methods have also been developed and these may be favored for low concentration epi-eDNA samples. Once samples have been taken, separating target cells from non-target environmental debris may prove challenging and expensive, though could be possible with cell sorting techniques such as a fluorescence-activated cell sorter (FACS) for tissue-specific and species-specific cells (Birnbaum et al., 2005; Smallwood et al., 2014). However, FACS is more efficient with live cells, as fluorescent markers will need to bind on extracellular proteins which could degrade over time in the environment. There may be limitations to what inferences science can make when only obtaining a snapshot of a community based on live cells present in a sample. Once cells have been obtained, single-cell epigenomics sequencing methods are possible, though more development is needed (Guo et al., 2013; Clark et al., 2016). Untangling the sequencing output with bioinformatics for epi-eDNA, beyond initial laboratory work, may present a challenge. Sorting reads according to species, individual, and/or tissue type may prove even more difficult than standard eDNA population genetics. As yet, no bioinformatic pathways have been successfully established for epi-eDNA using either single-species or metabarcoding approaches, but this area of eDNA research is ripe with possibility.

eDNA and Water Chemistry

Ecosystems are composed of an interplay between biotic and abiotic factors. Describing how abiotic factors influence and constrain biotic communities, and how these in turn shape abiotic surroundings is just one facet of ecosystem ecology. For example, abiotic factors can shape animal behavior (Kleinhappel et al., 2019), and animal behavior changes the environment (Deegan, 1993; Roman et al., 2014). If eDNA is to be analyzed to describe these processes, then teasing out how both biotic and abiotic factors shape the shedding and degradation, the "ecology" of eDNA is important.

One factor to consider may be that organismal behavior is affected by seasonal changes. Seasonal activities likely affect the amount of eDNA shed by some organisms, for instance, due to increased movement, gametes release, or life cycle stage, which consequently influences eDNA detectability (Klymus et al., 2015; Spear et al., 2015; Bylemans et al., 2017). Indeed, the migration of some organisms shows different eDNA signatures during different seasons, even indicating variation in community assemblage (Stoeckle et al., 2017; Xu et al., 2018).

In addition to the release of eDNA, seasonally variable abiotic factors such as temperature and UV may also speed or slow degradation (Strickler et al., 2015; Buxton et al., 2017). There have been mixed results on the influences of temperature and UV on eDNA degradation and evidence suggests that perhaps the main influences on eDNA degradation may not come from these sources alone (Strickler et al., 2015; Buxton et al., 2017; Mächler et al., 2018; Salter, 2018). Notably, microorganisms are an influential part of marine communities. Besides their broad role in the trophic cascades, ecosystem services, and gut microbiota, they influence the degradation of eDNA as well. In the environment, when microorganisms are nutrient limited, they will consume eDNA for phosphorous and, thus, speed up the degradation process (Salter, 2018). Additionally, there is evidence that eDNA can travel to areas through diet of predatory animals (Guilfoyle and Schultz, 2017). Therefore, further characterizing

the role microorganisms play on eDNA as well as how that interacts with abiotic factors are important pathways to elucidate.

With an increase in atmospheric CO_2 concentrations, ocean acidification and global warming likely also influences eDNA shedding and degradation. The increase of dissolved carbon dioxide and subsequent reduction of bioavailable calcium carbonate ($CaCO_3$) influence behavior of marine organisms, which may then influence eDNA release (Mostofa et al., 2016; Nagelkerken and Munday, 2016). For example, crabs in higher pCO_2 levels decreased foraging behavior (Dodd et al., 2015) and low pH can influence respiration rates in scallop (Liu and He, 2012). Increasing temperature has shown to increase metabolic rates as well (e.g., Eder et al., 2018). In combination with low food availability, this effect can even be strengthened (Eder et al., 2018). Besides indirectly influencing shedding rates of eDNA, evidence exists that very low pH can increase eDNA degradation, though effects are most likely to be seen with an increase in temperature and UV (Strickler et al., 2015). Potentially, ocean acidification should be considered when using eDNA as a tool for monitoring as high variability in pH may influence shedding rate or degradation, and, therefore, species detection.

Besides these influences on eDNA, a suite of geochemical corollaries is often used to describe ecosystems health. Indeed, a large body of literature has been dedicated to analyzing these interactions, and eDNA methods are only one technique used to describe biological community diversity within a suite of tools (Levin et al., 2009; Pan and Wang, 2012; Lowe et al., 2016; Mostofa et al., 2016). For example, planktonic and microbial communities may differ depending on differing dissolved organic matter found in an environment (Kujawinski, 2011; Osterholz et al., 2016; Laroche et al., 2018). A healthier, more diverse community correlates with increased dissolved oxygen (He et al., 2019). Flow of water may also influence dissolved oxygen content and, thus, community composition (Pochon et al., 2015). Besides dissolved oxygen, patterns of biodiversity have also been examined when they correlate with trace metals, for instance, toxic sulfides (He et al., 2019). Indeed, less alpha diversity was found with higher sulfide concentration using eDNA methods (He et al., 2019). Under harsher conditions, more sensitive fauna may not be as supported, and, thus, ecosystem function overall may decline (Lohrer et al., 2012). Through better understanding the interactions between biotic communities and these geochemical factors, we can better assign the ecological function of these communities and ecosystems.

eDNA and Hydrodynamics

Hydrodynamic modeling allows for the characterization of oceanic currents and, therefore, can help to answer ecological questions. For example, passive drift of larvae or other planktonic organisms can be revealed (Skliris and Djenidi, 2006; Leis, 2007; North et al., 2008). Combining such insights with genetic data, findings can resolve complex issues of ecological research. The genetic variation in the kelp *Laminaria digitata* along the Irish coast were underpinned by hydrodynamic distances (Brennan et al., 2014). Populations that were connected through currents had higher genetic similarity than populations that were separated by currents, even though sometimes the non-connected populations were located closer together. Even the occurrence of hybrid zonation, for example, hybrids between the mussels *Mytilus edulis* and *Mytilus trossulus* in the Baltic Sea, can be revealed by combining genetical approaches with hydrodynamic modeling (Stuckas et al., 2017).

There has been some work done to model eDNA transportation in freshwater riverine networks and in marine settings (Carraro et al., 2018; Andruszkiewicz et al., 2019; Fremier et al., 2019). Environmental DNA can be used to track organismal movement such as migration, as well as spatial patterns (Levi et al., 2019). Nearshore tides may only marginally influence the eDNA signal (Kelly et al., 2018; Murakami et al., 2019), most likely, the eDNA signal stays within 30 m of an organism in a marine setting within a few hundred meter from the shoreline (Murakami et al., 2019). Andruszkiewicz et al. (2019) modeled eDNA transportation in a distance of 15-20 km from the shoreline in Monterey Bay, CA, United States. They could show that eDNA is likely to be transported up to 40 km from the source. Various studies showed that decay rates are higher close to the shoreline than offshore, but variation in half-life times are quite large in the different study systems (Collins et al., 2018). Due to global variations of hydrodynamic patterns, further combined modeling of hydrodynamics and eDNA persistence is needed. This can be used to better link eDNA and animal activity.

Animal behavior itself can also alter the occurrence/persistence of eDNA. Currents and tides influence the activities of organisms, such as upwellings of nutrient-rich waters (Ryther, 1969; Block et al., 2011). For example, seasonal and vertical migration may be influenced by hydrodynamic movements which influence animal behavior (Batchelder et al., 2002; Croll et al., 2005). These behavioral changes may, in turn, influence eDNA signal. However, one possible false positive source that has not been quantified is the influence of dead organism eDNA in a marine setting (Kamoroff and Goldberg, 2018). Indeed, eRNA has been suggested for examining a shorter time frame (Pochon et al., 2017), though more recent work has suggested that aqueous eDNA stays in the marine environment on the scale of hours (Baker et al., 2018; Murakami et al., 2019). These studies highlight the need to be conscious of how biotic factors shape eDNA once released into the environment.

eDNA and Automated Sampling

Recent developments in technology have led up to an interest in automated eDNA sampling. Already, sampling has been assisted with automated, robotic technology to detect the presence and density of target organisms (Marques et al., 2013; Stern et al., 2015). Unmanned aerial vehicles can already collect whale breath samples for respiratory tract microbiome analyses (Pirotta et al., 2017) and collect water samples (Ore et al., 2015). One advantage of using robotic technology is the ability to leave an automated sampler out in the field for a period of time while still reliably taking samples at regular intervals, standardizing data collection (Marques et al., 2013). This reduces spatial and temporal variation in the data, which, for difficult-to-sample areas such as the open or arctic oceans, may be beneficial.

Sampling like this has already been done for microbiological samples (Scholin, 2010). These systems can be applied for sampling eDNA. Yamahara et al. (2019) sent an autonomous underwater vehicle with an environmental sample processor out in Monterey Bay. In addition, they performed traditional eDNA samples and compared the results, without significant differences. This first approach needs to be tested and quantified across multiple ecosystem dynamics for reliable results.

Besides presence-absence data, more measurements could be obtained using unmanned vehicles. For example, automated underwater qPCR (quantitative PCR, quantifies the abundance of target DNA fragments) sampling has been used to detect cyanobacteria abundance (Preston et al., 2011; Ussler et al., 2013). Based on this development, automated probe-based qPCR for eDNA could be developed for identifying specific species, such as endangered or invasive species of interest. Further research would be needed to create and sequence libraries autonomously in a field setting. The advent of MinION nanopore sequencing may aid in this development given their already successful sequencing results under remote field conditions (Pomerantz et al., 2018; Truelove et al., 2019). Once set up, the maintenance of such a system may reduce personnel hours spent in the field or in difficult-to-sample places, such as the open oceans or hydrothermal vents.

Another elegant solution is to use natural sampling units. Mariani et al. (2019) successfully used the filtration characteristics of sponges to capture eDNA from biotic communities of the surrounding area. Using natural structures may be a more sustainable research approach as opposed to high-tech instruments, which are likely costly and contain plastic that degrades and pollutes. Using these natural solutions may help to protect our oceans from further pollution such as microplastics.

CONCLUSION

Understanding changes in biodiversity and its impact on ecosystem services is just beginning. More data are needed to fully understand complex ecosystem processes (IPBES, 2019). The use of eDNA-based methodologies can offer a wide range of data collection opportunities, from monitoring species diversity, discerning diversity not captured by traditional methods and observing changes in community composition. The addition of eDNA data into spatio-temporal ecological modeling frameworks can help elucidate species distribution and migration patterns. If coupled with diversity and ecosystem data, ecological patterns and processes can be better understood. Thus, improved predictions regarding changes in species composition and its effect on ecosystem services can be made. Furthermore, the integration of life history characteristics of species can improve conservation success. Environmental DNA-based methods have a great potential as a cost and time saving methodology. When integrated into an interdisciplinary context, eDNA offers a variety of possible applications (**Figure 5**) with improved efficiency in contrast to traditional methods. Currently, the field is rapidly exploring and expanding into population-level data from eDNA with implications for discerning evolutionary patterns. Future developments may include a foray into epi-eDNA to fully utilize all information obtainable from DNA molecules. This may give us a lens into the patterns and processes of genetic change within and across species. The continued development of eDNA may prove valuable for answering ecological and evolutionary questions efficiently and effectively.

AUTHOR CONTRIBUTIONS

YS had the idea, wrote the sections "Marine Management and Ecosystem Functioning" and "Marine Conservation," and created the figures. CIMA wrote sections "Anthropogenic Influences on Marine Communities" and "Interdisciplinary Future of eDNA Monitoring." Sections "Introduction" and "Conclusion" were written jointly. Both authors contributed to the article and approved the submitted version.

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