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Incorporating Biological Traits into Conservation Strategies

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Abstract

Implementation of marine conservation strategies, such as increasing the numbers, extent, and effectiveness of protected areas (PAs), can help achieve conservation and restoration of ocean health and associated goods and services. Despite increasing recognition of the importance of including aspects of ecological functioning in PA design, the physical characteristics of habitats and simple measures of species diversity inform most PA designations. Marine and terrestrial ecologists have recently been using biological traits to assess community dynamics, functioning, and vulnerability to anthropogenic impacts. Here, we explore potential trait-based marine applications to advance PA design. We recommend strategies to integrate biological traits into (*a*) conservation objectives (e.g., by assessing and predicting impacts and vulnerability), (*b*) PA spatial planning (e.g., mapping ecosystem functions and functional diversity hot spots), and (*c*) time series monitoring protocols (e.g., using functional traits to detect recoveries). We conclude by emphasizing the need for pragmatic tools to improve the efficacy of spatial planning and monitoring efforts.

INTRODUCTION

Biological traits represent morphological, biochemical, physiological, structural, phenological, behavioral, and ecological characteristics of organisms, whether individuals or species (Diaz & Cabido 2001). Attributes such as motility, body size, life span, trophic mode, reproduction modalities, and habitat characterize the ecological roles that organisms play (Diaz & Cabido 2001, Violle et al. 2014) and interactions between individuals and species and the environment (Lefcheck et al. 2015). Traits are therefore useful to infer the responses of organisms to their environment and the effects of organisms on ecosystem processes (Violle et al. 2007, Nock et al. 2016). Functional diversity metrics are designed to capture the number, type, and distribution of biological functions across organisms (Diaz & Cabido 2001), with the potential to advance mechanistic understanding of how ecological communities assemble and function. Both individual and species traits can underpin metrics of functional diversity—indices that describe the total variation in one or more traits across all species within a community (Faith 1996). Individual traits describe variation across populations—for example, by quantifying the average or range of trait values (such as individual body size) across all individuals—whereas species traits (such as maximum body size) typically integrate across populations.

Biological trait–based approaches can clarify the mechanisms underlying the dynamics of ecological communities (Dray et al. 2014) and link species geographical distributions to their environment (Usseglio-Polatera et al. 2000, Bremner et al. 2006b, Jeliazkov et al. 2020). Functional trait diversity metrics also enable deeper insights into the role of diversity in the provisioning of ecosystem functions and services (Norberg 2004, Hooper et al. 2005, Vogt et al. 2010, Weithoff et al. 2015, Tavares et al. 2019) and the resilience of biological communities (Walker et al. 1999, Petchey & Gaston 2002). Indeed, numerous studies indicate that trait-based functional diversity indices predict ecosystem functioning more effectively than taxonomic diversity (e.g., Diaz & Cabido 2001, Bremner et al. 2003, Hooper et al. 2005, Anton et al. 2010, Loreau 2010, Schleuter et al. 2010, Mouillot et al. 2011, Mora et al. 2015, Törnroos et al. 2015, Villnäs et al. 2018). Biological traits of organisms ultimately link to ecosystem functions, including ocean nutrient cycling (Norkko et al. 2013, Belley & Snelgrove 2016), primary production (Lohrer et al. 2015), secondary production (Bolam & Eggleton 2014), and sediment erodibility (Harris et al. 2015).

Biological trait–based approaches incorporate diversity, functions, and responses to environmental conditions. These approaches, therefore, characterize populations, communities, and processes simultaneously in a framework that can inform conservation strategies through numerous pathways. Increasingly, protected areas (PAs), including marine protected areas (MPAs), marine reserves, and parks, are recognized as a key management tool to achieve sustainable use of resources and to preserve and restore ocean health (Gaines et al. 2010, Veitch et al. 2012). Global prioritization of protection punctuates the need to improve our capacity to prioritize which species, processes, and regions to protect, and to track progress following conservation actions. Many countries now strive to increase the number and extent of PAs to meet international targets. For example, the Aichi Targets developed by parties to the Convention on Biological Diversity aim to expand protection of the ocean to 30% by 2030. Efforts must prioritize the creation of well-designed and well-managed PAs that effectively protect and conserve natural systems (De Santo 2013, Roberts et al. 2018). PA success in achieving conservation objectives hinges on incorporating clearly defined ecological criteria and scientific information at the design stage, rather than primarily socioeconomic factors (Roberts et al. 2003). The criteria also need to advance beyond simple consideration of individual species or features of habitats and taxonomic diversity, such as species richness, endemism, and vulnerability (Brooks et al. 2006, Jenkins et al. 2013). Focusing on species or habitats may underrepresent biologically unique species and their ecological roles

within systems (Brum et al. 2017) and does not address how the suite of ecosystem components responds to different threats (Bremner 2008).

Incorporating approaches that consider the biological traits of organisms in PA design and evaluation increases the potential to achieve greater conservation gains (Bremner et al. 2006a,b; Bremner 2008; Frid et al. 2008; Strecker et al. 2011; Brum et al. 2017). Specifically, biological traits can improve marine conservation efforts (Bremner 2008, Vandewalle et al. 2010) by providing information on the diversity, structure, and dynamics of ecological communities and the associated ecological functions (Usseglio-Polatera et al. 2000). Trait-based approaches also complement biodiversity patterns based on taxonomic diversity, including identification of new hot spots of diversity (Stuart-Smith et al. 2013), and can help predict the responses of biological communities to current and future human impacts, including fishing and climate change (Bremner et al. 2004, 2006b; Darling et al. 2010; Beauchard et al. 2017).

Trait-based metrics in PA design build on the use of ecosystem-based management approaches that establish PAs to protect specific functions and associated services (Foley et al. 2010, Villnäs et al. 2018). In addition, metrics based on biological traits provide a common currency of diversity that transfers across species and habitats (Vandewalle et al. 2010), enabling comparisons of functional biodiversity across geographic locations (Statzner et al. 2001, Hodgson et al. 2005). Therefore, trait-based approaches offer a valuable tool to identify ecologically important areas, PA boundaries, and conservation objectives (Frid et al. 2008) and even to develop monitoring protocols. However, despite the potential applicability of biological traits in conservation, there are few examples of the use of trait-based approaches to develop conservation strategies and inform PA design. Challenges include a lack of rigorous trait data for many species and logical methods that include traits (Lefcheck et al. 2015); these deficiencies may limit uptake by scientists and managers.

Here, we explore the potential for trait-based applications to advance marine spatial planning efforts. We begin by providing a general overview of biological traits in the context of conservation (**Figure 1**). We review uses of biological traits in PA design and monitoring protocols, highlighting how management can use biological traits to help improve the efficacy of PAs to meet conservation objectives. We recommend integrating traits into conservation strategies, including assessments of the sensitivity and vulnerability of communities to human impacts, predictions of species extinction risk, and the identification of resilience in natural systems. Traits can also inform PA spatial planning in mapping new hot spots of diversity and functions and in developing monitoring protocols that are responsive to population and community change. We further explore the advantages of trait-based approaches over traditional taxonomic approaches. We then address the challenges of transferring concepts and approaches developed on land to the ocean, recognizing intrinsic differences between the realms and logistical difficulties specific to marine conservation. We conclude by emphasizing the importance of including functional diversity metrics based on biological traits in PA planning and the need to identify pragmatic tools applicable to different contexts to support spatial conservation planning and monitoring efforts.

COMMON APPROACHES FOR INCORPORATING BIOLOGICAL TRAITS IN ECOLOGICAL STUDIES

In the last 50 years, scientists have used biological traits of organisms to characterize biological communities and gain insights into how communities function. In the early 1970s, plant ecologist J. Philip Grime (1974) incorporated traits of species to classify vegetation based on species strategies and to predict disturbance levels at particular sites. Subsequently, Southwood (1977) formulated the habitat templet theory, hypothesizing that the characteristics of the habitat select and favor specific sets of individual characteristics that determine which organisms persist.
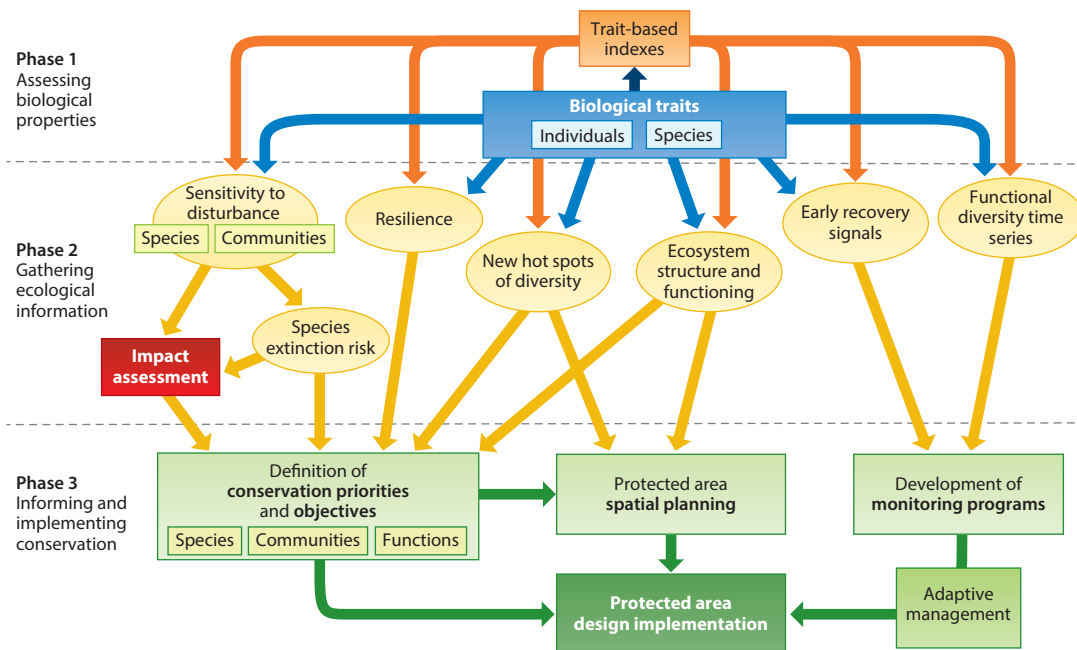
Figure 1

Phases for integrating biological traits into conservation strategies. These phases include the assessment of biological properties of populations and communities (phase 1); the gathering of ecological information on the vulnerability, structure, functioning, and responses of systems (phase 2); and the implementation of protected area design by informing prioritization, spatial planning, and monitoring protocols (phase 3).

Southwood's work inspired other scientists to use traits in terrestrial and marine ecology. Traits have also been used to predict species distributions and community structure among habitats and along environmental gradients (Bournard et al. 1992, Townsend & Hildrew 1994, Townsend et al. 1997). For instance, Charvet et al. (1998a,b) used traits of macroinvertebrates to develop biomonitoring tools in freshwater streams by linking the trait patterns of a diverse set of species to environmental data.

Functional indices, such as functional diversity (the variation in one or more biological traits across all species within a community; Faith 1996), offer one way to incorporate biological traits into ecological studies. Other traditional functional indices include metrics based on the sum (Walker et al. 1999) or average (Botta-Dukát 2005) of functional distances between species pairs in multivariate functional trait space, the distances between species along hierarchical classification (e.g., Petchey & Gaston 2002), or the distribution of abundance along functional trait axes (e.g., Mason et al. 2003).

The scientific community lacks a consensus on which index to use to quantify functional diversity because functional diversity encompasses at least four components. Some researchers argue that the first three—richness, evenness, and divergence—require separate quantification (Mason et al. 2005, Villéger et al. 2008). Functional redundancy adds a fourth dimension of diversity to trait analysis: species with overlapping ecological roles in communities and ecosystems (Lawton & Brown 1993). Indeed, the presence of many functionally similar species in a given habitat, known as the portfolio effect (Doak et al. 1998), may protect against functional loss where changes in the community impact one or more species.

In some cases, functional group richness is used as a surrogate of functional diversity (even though richness is acknowledged as representing only one dimension of function diversity). Species are assigned to functional groups based on a few general and well-known key attributes, and specialists estimate the frequency of these categories through indices such as the Shannon or Simpson index (Stevens et al. 2003, Villéger et al. 2008). However, this approach ignores species abundances and functional differences among species (Fonseca & Ganade 2001, Villéger et al. 2008). Alternatively, some studies define subgroups of traits that describe specific functions or ecosystem properties and use them to estimate the cumulative expression of ecosystem properties at individual sites and, at larger scales, ecosystem multifunctionality, which refers to multiple, interacting functions in an environment (Villnäs et al. 2018). Other approaches use multiple functional traits (e.g., body size, mobility, feeding strategy, habitat, and reproductive mode) measured for each individual or species and statistical techniques such as principal component analysis or co-inertia analysis to distinguish different communities and their associated functions (Bremner et al. 2003, Petchey & Gaston 2006). Such approaches may add significant challenges in obtaining specific trait values for every species in a community, especially rare species, but offer a more complete understanding (Schleuter et al. 2010). In fact, analyses that include only some of the species that are present in a system and only a few traits (e.g., feeding type or physiological tolerance) by definition exclude potentially important ecological information (Charvet et al. 1998b).

Biological trait analysis (Bremner et al. 2006b) offers a comprehensive approach to describe multiple aspects of functioning based on features of the biological communities, links traits to environmental conditions, and predicts associated changes in ecosystem processes performed by communities (e.g., nutrient regeneration and processing of pollutants in marine sediments). The analysis uses multivariate ordination to describe patterns of trait composition across all species within the entire assemblages, incorporating both multiple traits and multiple trait categories. While species are typically scored as falling within one trait category (e.g., feeding type has categories of deposit feeder, filter/suspension feeder, opportunist/scavenger, and predator), fuzzy coding allows species (or the taxonomic unit of interest) to fit into more than one trait category. Fuzzy coding, therefore, quantifies the affinity of a species across different categories of a trait. The analysis can then include the abundance or biomass of species as a weight and empirically describe differences in ecological strategies or functioning among communities. The traits that contribute most to these differences can subsequently be identified and linked with other variables, such as environmental parameters and anthropogenic stressors.

Biological traits also vary among individuals, sometimes even more than among species. Intraspecific trait variability results from either phenotypic plasticity or genetic diversity, where selection filters lead to population adaptations to local environments (Jung et al. 2010) and substantial shifts in ecological dynamics (Whitlock et al. 2007, Bolnick et al. 2011, de Bello et al. 2011, Lefcheck et al. 2015). Indeed, some species exhibit high intraspecific trait variability. For example, variation in several traits of European freshwater fish species, such as growth rate, mortality rate, and length of the breeding season, is greater among populations of the same species across latitudes than among species (Blanck & Lamouroux 2006). Some species exhibit much higher intraspecific variability in traits than others and, more predictably, variability among ontogenetic stages of a species. For example, individual body size predicts the trophic level of fishes better than species identity (Jennings et al. 2001).

Depending on the specific conservation context, it may be important to consider population-level trait variability. For instance, obtaining functional trait estimates from existing data that represent average values across the full range of conditions under which a species occurs may miss important intraspecific variation, and thus under- or overestimate sensitivity. In fact, species with high population-level diversity may respond and adapt more successfully to environmental

changes and therefore be more resilient to impacts. The importance of considering trait variability at the population level is particularly true if intraspecific variability is high or subpopulations are adapted to local conditions (e.g., Atlantic cod; Hu & Wroblewski 2008). Conversely, average species traits derived from small-scale (single-environment) studies may not account for altered phenotypes driven by local adaptations and therefore may inaccurately describe populations from different geographic areas (Bolnick et al. 2011, Tucker & Cadotte 2013).

The expression of biological traits can also vary within species over time, in response to natural or human-driven changes in environmental conditions (Jennings & Kaiser 1998). Incorporating intraspecific trait variability into trait-based community ecology may advance the theory on the ecological filtering processes that occur during community assembly by identifying which traits are successful (Jung et al. 2010). Intraspecific trait variability may also offer insights on stability and functionality (Bolnick et al. 2011). Indeed, authors now consider the functional variability of individuals within populations when interpreting ecological dynamics such as community composition, fitness, and competition (e.g., Bürger 2005, Kopp & Hermisson 2006, Vellend 2010, Bolnick et al. 2011).

Ultimately, integrating traits of individuals across species to describe communities offers the most accurate way to describe functional diversity and explain functional processes (Cianciaruso et al. 2009). This objective requires measuring traits from all individuals within a community during each sampling event (Cianciaruso et al. 2009), usually requiring prohibitive labor (Baraloto et al. 2009). A less intensive solution (de Bello et al. 2011) involves sampling a subset of the existing population of each species to capture representative trait distributions. Fuzzy coding approaches (described above) allow variation in trait categories within taxa (Chevenet et al. 1994) and partially incorporate such variation into the analysis when such variability is known. If the goal is to describe a community functionally, then individual trait expression can even be assessed without first identifying species taxonomically, such as in cases where similar species are difficult to distinguish. The nonnecessity for taxonomic expertise may, therefore, offer an advantage in terms of time and cost. In addition, the lack of available data on traits for many species—or, more often, inaccuracy for certain populations—may require direct measurements of individual traits in populations of interest. By contrast, the difficulty or even impossibility of measuring some individual traits on preserved specimens may require drawing opportunistically from published data to attribute scores to traits representing, for instance, reproduction behavior, life span, and feeding habits. However, taxonomic biases in basic biological information limit mining the literature to well-studied species, such as most fishes and some macroinvertebrates. Therefore, a mix of new observations, expert opinion, and published data could yield robust information (Chapman et al. 2019).

THE RATIONALE FOR THE USE OF BIOLOGICAL TRAITS IN MARINE CONSERVATION

Traits to Identify Conservation Priorities and Inform Conservation Objectives

PA planning usually begins with the creation of databases and maps of ecological, physical, and socioeconomic characteristics of the region of interest. This information then underpins setting conservation objectives (**Figure 1**, phase 3), such as quantitative assessments of the minimum amount of a feature that needs to be conserved (Magris et al. 2017), including empirical targets for ecological outcomes (Game et al. 2013, Pressey et al. 2015). Conservation objectives define one or more feature targets for a PA, which can include sustaining species, biodiversity, ecosystem types, and functioning (Magris et al. 2017).

Traditional approaches used to inform conservation objectives fail to capture important aspects of functional diversity and ecosystem functioning. When developing conservation objectives in an area of interest, managers typically use taxonomic indicators, such as species richness and the presence of endemic and/or threatened species. This information is then combined with socioeconomic data on the level of human use and impact. For example, one conservation objective might focus on identifying the species that are most vulnerable or resilient to specific threats. Neglecting biological traits in this assessment, by definition, omits important ecological context (Moretti & Legg 2009, de Bello et al. 2010).

While no single parameter effectively describes the functioning of an entire ecosystem (Giller et al. 2004, Rees et al. 2012), biological traits offer advantages over traditional taxonomic approaches. First, traits represent information about the sensitivity of species and communities to disturbance (**Figure 1**, phase 2). Traits can predict species and community responses to changes because biological traits link directly to the fitness of organisms (Vandewalle et al. 2010). Therefore, species with traits that increase vulnerability to a given disturbance and/or lower trait redundancy typically dominate sensitive communities (Walker 1992, Williams et al. 2010, McLean et al. 2019a). Biological traits can also help researchers distinguish changes related to niche effects caused by anthropogenic or environmental stressors from random effects associated with natural community variability. This possibility exists because a disturbance tends to exclude or reduce the abundance of species with particular traits (Haddad et al. 2008). For example, McLean et al. (2019a) documented the high sensitivity of small pelagic and corallivorous fishes to ocean warming, where the trait structure and redundancy of temperate and tropical fish communities determined their respective sensitivities to a disturbance. Their study was among the first to use temporally and spatially expansive data, verifying the validity of considering biological traits to predict future disturbance impacts on biodiversity and ecosystem functioning across ecosystems and taxa (McLean et al. 2019a).

Second, based on the same principles that determine sensitivity, individual and species traits can help predict the extinction risk of populations and species (**Figure 1**, phase 2). These predictions can inform priorities for conservation, including species or communities in locations not yet threatened, perhaps because current levels of anthropogenic pressure have not reached a critical level (Cardillo et al. 2006, Van Kleunen & Richardson 2007, Cooke et al. 2019). These approaches offer the important advantage of distinguishing vulnerable species and detecting disturbance-related changes before local extinction occurs (Mouillot et al. 2013). For example, Cooke et al. (2019) used biological traits of more than 15,000 land mammals and birds to quantify current and predict future ecological strategies. Based on species' extinction probabilities, they predicted a change in strategies over the next 100 years, where mammal and bird species will shift toward becoming small, fast-lived, highly fecund, insect-eating generalists.

Third, traits can provide information on the capacity of natural systems to resist and recover after disturbances (i.e., resilience), which also merits consideration when defining conservation objectives (**Figure 1**, phase 2). Management decisions should prioritize safeguarding ecological resilience in order to create PAs that maintain desirable ecosystem states, even under changing environmental conditions (West & Salm 2003, Mori et al. 2013). High trait diversity or redundancy in communities usually indicates higher resilience to disturbances and invasions, whereas species diversity alone is not always a good indicator of resilience (Dukes 2001, Bellwood et al. 2004, Bates et al. 2019). Bregman et al. (2016) analyzed the functional trait structure of Amazonian forest bird assemblages to explore the impacts of land-cover change on two ecosystem processes that maintain the structure and resilience of human-modified tropical forests: seed dispersal and insect predation. Their findings suggest that the loss of tropical forests reshapes the types of species that are present in the landscape, with dramatic consequences for ecosystem processes and resilience.

They concluded that standard approaches used to understand environmental change based solely on species richness and composition may overlook important implications for ecosystem processes that functional diversity indices effectively capture (Bregman et al. 2016).

Fourth, biological traits can help to identify functionally important locations for protection (**Figure 1**, phase 2) in order to conserve biodiversity hot spots with species that play different ecological roles, and therefore functions and services (Frid et al. 2008, Stuart-Smith et al. 2013). For instance, comparison of fish biodiversity distribution based on traditional taxonomic metrics with those based on novel biological trait metrics identified new hot spots of functional diversity for reef fish in locations rarely prioritized for conservation, such as temperate rocky reefs (Stuart-Smith et al. 2013). Moreover, forecasts on how environmental change and anthropogenic activities impact ecosystem functions and associated goods and benefits provide a framework for informing PA designs that explicitly incorporate measures of ecosystem functioning where the intent is to protect or restore functional diversity and ecosystem services (Bremner 2008, Frid et al. 2008). Yet explicit consideration of functioning in conservation planning has historically lacked the fundamental science to support such an approach (Frid et al. 2008, Beauchard et al. 2017). In some circumstances, PAs originally designated to protect specific features of habitats and biodiversity also fortuitously protect ecosystem functions and services. However, this is not always the case. For example, locations designated to protect rare or threatened species may rank low in overall functional importance in comparison to other habitats or locations (Potts et al. 2014). In other cases, management measures may not adequately conserve species that critically underpin functionally important PAs. For example, higher taxonomic diversity may not always coincide spatially with higher functional diversity and ecosystem functioning (Stuart-Smith et al. 2013).

Fifth, it is possible to generalize indicators based on biological traits (Vandewalle et al. 2010), enabling biodiversity comparisons among regions differing in biogeographies, communities, and species composition (Statzner et al. 2001). As a result of environmental filtering, communities tend to be composed of species with similar traits (Poff 1997, Statzner et al. 2001, Bremner et al. 2006b, Hewitt et al. 2008, Tolonen et al. 2016), which therefore leads to similar responses to the same anthropogenic stresses in communities from different regions (Statzner et al. 2001). Indeed, McLean et al. (2019b) showed temporal trait convergence in North Sea fish communities in response to ocean warming, despite divergence in species composition. This convergence in species with similar traits enables the development of general models of population and community dynamics and distributions of organisms within their environment that have widespread applicability (Blanck & Lamouroux 2006, McGill et al. 2006, McLean et al. 2019b). Therefore, indicators based on traits can be particularly useful for environmental policies implemented across large geographic areas, where differences in species composition could otherwise complicate traditional, species-based assessments (Bremner et al. 2003, Villnäs et al. 2018). Examples include designing large PAs that encompass multiple biogeographic realms, comparing biodiversity among regions in order to define conservation priorities, and tracking how these communities develop following protection and with exposure to disturbance events.

Following the identification of priorities and objectives for conservation, spatial planning of PAs (**Figure 1**, phase 3) requires defining details such as PA size, boundaries, and allowed activities. Planning stages should aim to include conservation priorities and meet specific objectives. Ideally, PAs should be as large as possible (Edgar et al. 2014). Networks of PAs are critical to protecting habitats important for different life history stages and population connectivity (Cowen & Sponaugle 2009, Burgess et al. 2014). Traditionally, PA spatial planning has focused on the spatial distribution of key species or habitats, despite the dynamic and ecologically connected nature of marine systems, in which ecological processes extend across physical habitat boundaries (Frid et al. 2008). In marine systems, biological assemblages may depend on processes occurring elsewhere
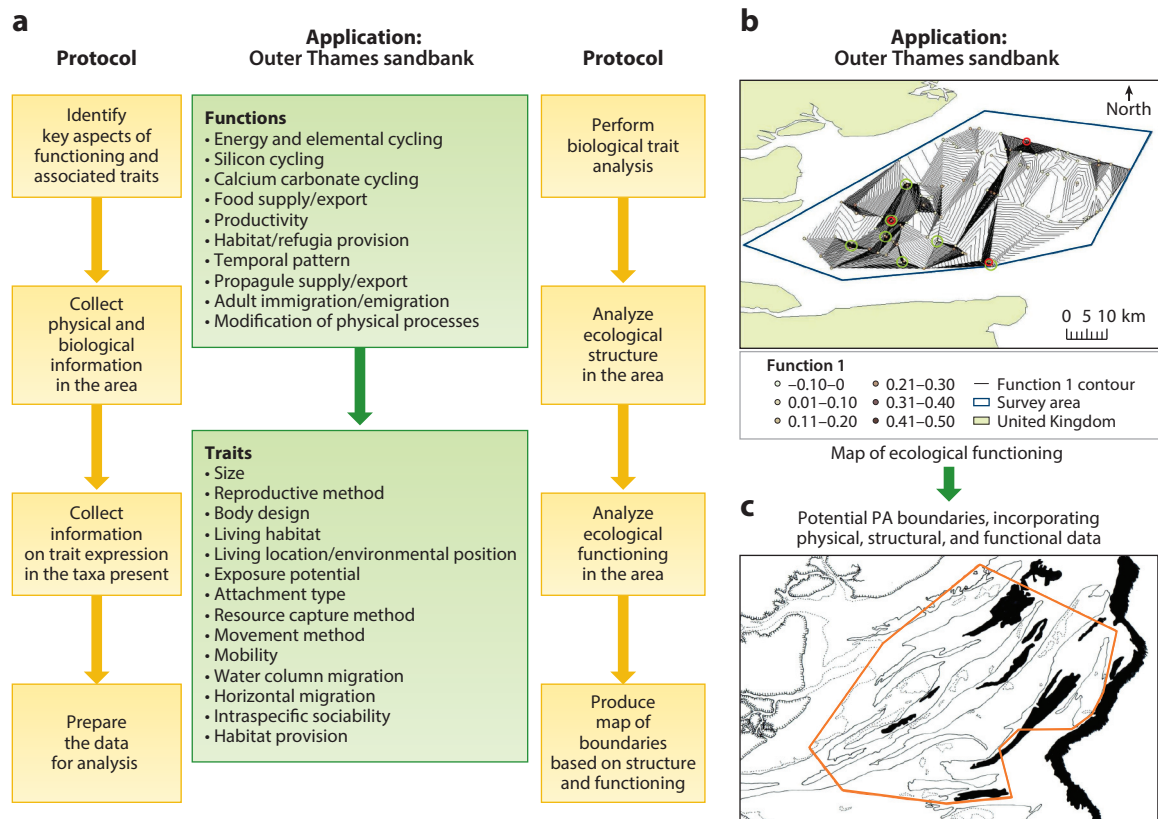
Figure 2

(*a*) Key steps in the protocol used by Bremner et al. (2006b) to explicitly include ecological structure and functioning in delimiting the boundaries of special areas of conservation through biological trait analysis, along with examples of the relevant functions and traits in an application of such a protocol to the Outer Thames sandbank in the United Kingdom. (*b*) Map of ecological functioning in the Outer Thames sandbank based on the co-inertia scores of the biological communities. Lines close together indicate the areas of greatest change, and lines farther apart indicate areas of similarity. Data points circled in red indicate outliers, whereas those in green indicate sampling of the same or adjacent locations using different techniques. (*c*) Potential PA boundaries based on physical, structural, and functional data, including the results shown in panel *b*. Abbreviation: PA, protected area. Panels *b* and *c* adapted with permission from Bremner et al. (2006b).

(Balbar & Metaxas 2019). For example, distant locations may play a central role in supplying food, nutrients, and reproductive propagules, and migratory residents that leave the PA may be at risk (Morris et al. 2014). Therefore, the simple protection of physical habitats can be insufficient to preserve processes, and biological traits can help in identifying ecologically relevant locations for specific conservation objectives (Frid et al. 2008).

PA zoning should maximize protection for ecologically critical species, communities, and processes (Agardy 2000). A case study from Bremner et al. (2006a) illustrates a protocol and practical application of biological traits in proposing PA boundaries (**Figure 2**; see also the sidebar titled The Potential of Using Biological Trait Analysis to Inform Protected Area Design). The protocol could potentially advance conservation outcomes because it explicitly considers the occurrence of functions provided by biological communities in designing PAs. However, managers have not generally embraced the use of biological traits to advance marine conservation outcomes. This reluctance may reflect the lack of accessible information and protocols on species

THE POTENTIAL OF USING BIOLOGICAL TRAIT ANALYSIS TO INFORM PROTECTED AREA DESIGN

Bremner et al. (2006a) used biological trait analysis based on species to explicitly incorporate the ecological structure and functioning of benthic communities in delimiting PA boundaries. They described multiple aspects of functioning using features of the biological ecosystem components and selected species traits as indicators of functions. Specifically, they examined frequencies of species traits across assemblages to determine the ecological structure and functioning of assemblages and how these relate to environmental parameters. To demonstrate a practical application of the protocol they developed, they applied it to two of the proposed Offshore Special Areas of Conservation in the United Kingdom (the Outer Thames sandbanks and the Eddystone Reef). The protocol enabled the generation of maps of ecological structure and functioning, which were used to delineate the boundaries of potential PAs that aimed to protect biological communities and the functions they support (**Figure 2**).

Similarly, Rees et al. (2012) developed a framework that used biological trait analysis to incorporate indirect ecosystem services into PA planning and management and highlight the potential of biodiversity to provide indirect ecosystem services. The authors used their framework to define the spatial area over which benthic species deliver specific indirect services (in this case, nutrient cycling, gas and climate regulation, and bioremediation of waste) in Lyme Bay in southwest England. This approach enables managers to link the provision of services with current conservation policies (Rees et al. 2012).

These case studies demonstrate applications of biological trait analysis and indicate that simply considering habitat type or biodiversity measures when selecting PA boundaries ineffectively characterizes ecosystem function and services. They concluded that because ecological processes typically transcend physical habitat boundaries, an effective PA design should consider biological communities and associated functions (Bremner et al. 2006a, Frid et al. 2008). Also, conservation policy that focuses on biodiversity alone may result in the exclusion of functionally important but low-diversity locations during the planning process (Frid et al. 2008, Rees et al. 2012).

traits for conservation. Analyses can also be time-consuming (see the sidebar titled Why Don't Managers Embrace Biological Trait Analysis in Spatial Planning?).

Monitoring Outcomes in Protected Areas: Using Biological Traits to Track Effects of Protection

Enhancing PA effectiveness in achieving conservation goals hinges on the development and use of adequate and comprehensive indicators that measure the socioeconomic, biophysical, and institutional (governance) outputs and outcomes of PA management. Evaluation, or monitoring (**Figure 1**, phase 3), consists of reviewing the results of management actions and assessing whether these actions produced the desired outcomes (Pomeroy et al. 2005). This important step allows management to respond and adjust actions based on actual outcomes. Obtaining information about the conditions and changes that occur in PAs and assessing the effectiveness of management actions require a periodic and comprehensive assessment of the natural and social processes that occur within and outside PA boundaries.

Indicators based on traits can detect early responses, including important recovery signals (Mouillot et al. 2013, Coleman et al. 2015) (**Figure 1**, phase 2), to help assess the outcomes of protection. Where needed, trait indicators also allow rapid, adaptive management measures. Detection of responses of traditional metrics based on taxonomic diversity such as species richness or abundance sometimes takes up to 20 years (Edgar et al. 2009, Babcock et al. 2010) because subtle community-level changes, changes in long-lived species, or system variability may mask earlier detection (Coleman et al. 2015). In fact, trophic or functional changes often drive recovery following

WHY DON'T MANAGERS EMBRACE BIOLOGICAL TRAIT ANALYSIS IN SPATIAL PLANNING?

Biological trait analysis is one tool to quantify ecological functioning (Frid et al. 2008), with potential application to marine conservation in the design and management of PAs aimed at protecting functions provided by biological communities (Bremner et al. 2006b) and associated ecosystem services (Rees et al. 2012). Biological trait analysis can highlight changes in species composition arising from anthropogenic factors that impact ecosystem functioning (Rees et al. 2012). Despite its potential, however, it has not been embraced by managers for marine spatial planning.

Challenges include a lack of rigorous trait data for many species and logical methods that include traits (Lefcheck et al. 2015). In addition, the time- and data-consuming nature of biological trait analysis may discourage managers from applying such a methodology when planning PA design and management. Another downfall of this approach is that, by itself, trait analysis does not quantify the associated functioning and associated ecosystem services delivered. In fact, no methodology can quantify how much "function" biological assemblages deliver or is required to ensure human well-being. Therefore, integrating ecosystem services into conservation planning and management remains a significant challenge (Rees et al. 2012). Acknowledging the need to keep working toward pragmatic tools to include ecosystem functions and services in marine conservation plans, managers could consider biological trait analysis as a current tool to advance marine conservation, which will progress as open trait databases are produced.

protection (Babcock et al. 2010). For instance, large and predatory species often benefit directly from protection, leading to indirect community shifts as trophic levels are restored (Babcock et al. 2010, Coleman et al. 2015). Therefore, indicators that include biological traits often prove more sensitive in detecting early and subtle responses following protection, in addition to providing important information on key ecosystem processes (Mouillot et al. 2013).

PA monitoring that includes measuring the biological traits of species through time (**Figure 1**, phase 2) can, therefore, track the effects of management interventions and, when compared with a control site, allows attribution of protection from other variables that also shift through time, such as warming (e.g., Bates et al. 2014b). Trait-based approaches can provide information on changes in the functionality of assemblages over time and confirm whether protective measures resulted in positive effects on functioning (de Bello et al. 2010, Vandewalle et al. 2010). Traits also offer an alternative for determining reference (or baseline) conditions, including functional aspects (Bremner 2008, Bates et al. 2014a). Consideration of functional traits can help discern changes related to natural community assembly processes, associated with environmental shifts, and caused by anthropogenic stressors (e.g., Usseglio-Polatera et al. 2000, Bremner et al. 2006b). For instance, de Bello et al. (2012) used biological traits of plants to discern niche differentiation effects (resulting in trait divergence) from competition effects (resulting in trait convergence) on species coexistence and community assembly. Understanding the mechanisms driving changes in biological assemblages over time is particularly important when evaluating conservation outcomes for attribution and context.

Conservation in a Changing World: How Biological Trait–Based Approaches Can Help Mitigate Against Ecosystem Change

PA design rarely incorporates climate change–related disturbances (Levy & Ban 2013, Bates et al. 2019). The legislation around management tools such as MPAs also typically lacks the flexibility to support adaptive management needed to cope with change. Conservation in a changing world should prioritize designing PAs that enhance ecosystem resilience to climate change (McLeod et al. 2009). The role of climate as an increasingly significant stressor in both terrestrial and marine

ecosystems leads to biodiversity loss, shifts in communities, and species extinctions (Pereira et al. 2010, Doney et al. 2012, Bijma et al. 2013, Antão et al. 2020). Although the creation of PAs alone cannot fully mitigate the effects of climate change, protection from other threats can minimize the synergistic impact of multiple stressors, ultimately increasing ecosystem resilience to climate change impacts (Trakhtenbrot et al. 2005, Bates et al. 2019). Nonetheless, climate change can threaten the effectiveness of conservation by altering species distributions, community structure, and ecosystem properties of the established or planned PAs (Pressey et al. 2007).

Traits of species link directly to their sensitivity or adaptability to climate change (Jiguet et al. 2007; Dawson et al. 2011; Foden et al. 2013; Bates et al. 2014a; McLean et al. 2019a,b). This linkage can help to predict ongoing and future effects of climate change when designing PAs. For instance, Foden et al. (2013) identified the main traits associated with increased sensitivity and low adaptability to climate change in birds, amphibians, and corals. These traits include habitat specialization, environmental tolerances, dependence on environmental triggers or interspecific interactions that climate change could disrupt, rarity, low dispersal ability, and limited capacity to evolve and adapt. Combining information on species sensitivity with predictions of climate change extent in different regions can help define population vulnerability and identify priority conservation areas. Traits can also predict climate change effects on ecosystem processes and functioning. For instance, Suding et al. (2008) proposed a framework that uses different functional traits to predict the effects of environmental changes on ecosystem functions.

In the same way that species traits can indicate sensitivity to climate change, traits can identify species with broad environmental tolerances and habitat requirements, strong competitors, and potential geographic spread (Kotiaho et al. 2005, Van Kleunen & Richardson 2007, McKnight et al. 2016, Cardeccia et al. 2018). Therefore, traits related to physiological tolerance, life history strategies (Sol et al. 2012), and biotic interactions (Dick et al. 2002, Twardochleb et al. 2013) can predict invasion potential (Blossey & Notzold 1995). For instance, Cardeccia et al. (2018) reported that high dispersal ability, high reproductive rate, and ecological generalization all characterized widespread nonindigenous species in European seas. Traits, therefore, provide the basis for tools that can simultaneously identify which species are most likely to become invasive in the future and which native species are most susceptible to negative effects of invasions. Thus, trait-based approaches can help focus conservation efforts on strategies that prevent the spread of invasive species and protect the most vulnerable native species.

CHALLENGES IN TRANSFERABILITY FROM TERRESTRIAL TO MARINE SYSTEMS

Marine conservation lags behind its terrestrial counterpart, in both the extent and effectiveness of conservation measures (Spalding et al. 2008). As of May 2020, PAs covered only 7.4% of the ocean, compared with 15.2% of land (UNEP-WCMC & IUCN 2020). Furthermore, only 2.5% of the ocean received full protection (Mar. Conserv. Inst. 2020), with uneven representation across ecosystem types (Spalding et al. 2008). One issue is that the translation of methodologies developed for terrestrial conservation to marine areas rarely considers differences between the two realms (Allison et al. 1998, Carr et al. 2003, Hooker & Gerber 2004, Agardy et al. 2011). Marine systems fundamentally differ from terrestrial ones because the ocean covers most of the planet, with fewer physical boundaries to restrict dispersal (Hooker & Gerber 2004). These differences result in ecological processes in the ocean that span larger spatial scales, often with greater connectivity (Carr et al. 2003). Moreover, many marine species have open populations, where offspring disperse over long distances and parental populations rely on the immigration of propagules arriving from other sources. By contrast, most terrestrial species are direct developers, with offspring that do not disperse far from parental populations (Carr et al. 2003). Thus, marine

systems require larger, self-sustaining PAs or well-connected networks (Carr et al. 2003, Edgar et al. 2014).

Moreover, the hidden and relatively inaccessible marine environment (Edgar et al. 2016) creates greater challenges for sampling, observation, and manipulation of natural assemblages. Despite many technological and scientific advances in recent decades, such as seafloor observatories and genetic tools, research on and applications of biological traits in the marine environment are in their infancy for many taxa compared with those in the freshwater and terrestrial realms (Bremner 2008, Madin et al. 2016b, Beauchard et al. 2017). Understanding the general relationships among traits, species, and environments requires advances in marine research, including funding allocation, in order to generate ideas about how the approach can guide marine conservation and management (Edgar et al. 2016). For example, recent efforts are increasing the availability and reliability of information on species traits through curated and open-source databases of trait information, such as the Coral Trait Database for corals (Madin et al. 2016a) and sFDvent for hydrothermal vent species (Chapman et al. 2019).

In the ocean, even more than on land, logistical and financial constraints limit the scope of many studies in space and time and therefore the current understanding of ecological patterns, biodiversity, ecosystem functioning relationships, and even the occurrence of threats (Whittaker et al. 2001, Snelgrove et al. 2014, Edgar et al. 2016). In addition, marine ecosystems often incorporate diverse habitats and span environmental and anthropogenic gradients, complicating the extrapolation of local properties onto larger scales (Snelgrove et al. 2014). Thus, some of the approaches developed and tested in terrestrial systems that generalize from one region to another may be less accurate in dynamic marine systems. This problem also applies to biological traits because data collected in limited biogeographic areas form the basis of most trait databases. Such data may, therefore, represent populations from other areas and underestimate values for the species. Identifying different populations within a geographic region, though often complicated, may prove important when applying traits (as discussed above).

Even so, the potential to generalize results of trait-based analyses across similar habitats in different regions means that biological traits can help to address challenges in comparing vulnerability assessments, which often span different spatial scales (Vandewalle et al. 2010). Moreover, trait-based analyses are also applicable to a wide range of marine organisms and habitats (**Figure 3**), from coral reefs to deep-sea benthic sediments and the pelagic habitats in between.

FROM THEORY TO PRACTICE: RECOMMENDATIONS ON HOW TO PRACTICALLY INCORPORATE BIOLOGICAL TRAITS INTO CONSERVATION SCIENCE

Several major steps must occur in the creation of a new PA, and scientists and managers can incorporate biological traits into some of these steps (**Figure 4**; see also sidebar titled How Should Protected Area Design Incorporate Biological Traits?). Maximizing the benefits of using biological traits to inform PA design hinges on selecting the appropriate types and number of traits to include in the analysis, as well as the appropriate index or indices. We have four recommendations for how to do so.

First, traits and methodologies should be selected according to the key ecological questions that define conservation priorities. These questions might pertain to assemblage functioning, the presence and effects of anthropogenic impacts, or both (Bremner et al. 2006b). For example, feeding traits can be used as indicators of carbon transport between the pelagos and benthos (Frid et al. 2008). Similarly, some traits are more responsive than others to environmental change or anthropogenic impacts and can be used to detect community response signals (Coleman et al. 2015, Nock et al. 2016). Depending on the conservation objective, scientists can favor response
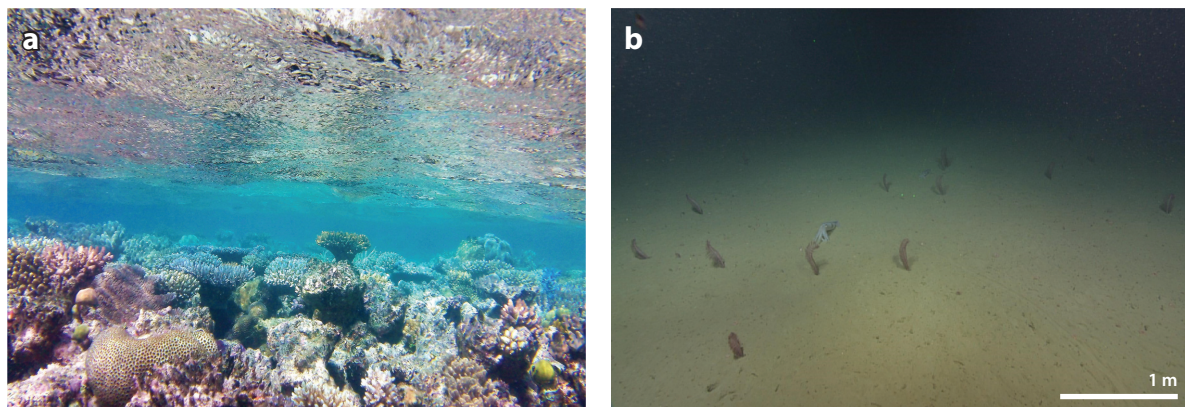
Figure 3

Example of marine habitats where biological traits can help advance marine conservation, illustrating the wide range of habitats for which managers could utilize trait-based approaches. (*a*) The Great Barrier Reef, Australia. Extensive trait databases exist for fishes and corals to aid such an application. Photo by Paul Snelgrove. (*b*) Deep-sea sedimentary habitats (the image shows approximately 15 m^2 of mud with the scattered presence of epifaunal sea pens) in the Laurentian Channel Marine Protected Area, Canada, where conservation efforts consider functions. Scattered sources exist on traits for different groups of sedimentary fauna, though most extensively for polychaete worms. Photo taken from the Remotely Operated Platform for Ocean Sciences (ROPOS), courtesy of the Canadian Scientific Submersible Facility (CSSF).

traits, which determine the response of organisms to environmental conditions, or effect traits, which determine the effect of organisms on ecosystem processes and functions (Lavorel & Garnier 2002). Finally, a useful trait generally varies among taxa, species, or individuals (McGill et al. 2006, Petchey & Gaston 2006, Lefcheck et al. 2015, Nock et al. 2016). However, trait categories shared among individuals, species, or higher taxa provide a means to quantify the degree of redundancy within assemblages and identify vulnerable communities and ecosystem components (Lefcheck et al. 2015). Selecting traits representing specific ecosystem functions or those that respond to certain environmental stressors may be a good way to standardize protocols to relate communities to ecosystem functioning or to detect anthropogenic impacts (Bremner et al. 2006b). However, further studies are necessary to expand our understanding of the relationships between traits and functioning (Maureaud et al. 2020).

Second, analyses should include multiple biological traits and diverse taxa that represent a broader perspective on ecological functioning and the effects of natural and anthropogenic factors
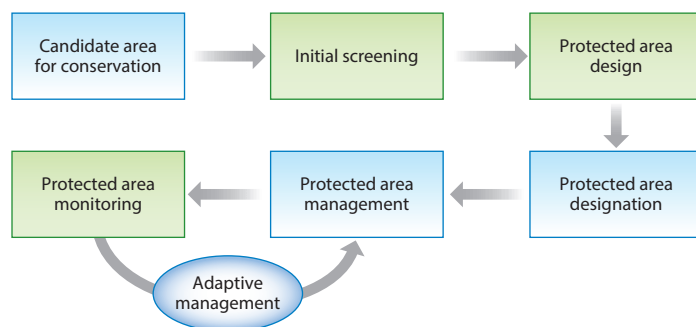

Figure 4

Key steps toward the creation of a new protected area. Green boxes highlight steps where the application of biological traits can enhance marine conservation outcomes.

HOW SHOULD PROTECTED AREA DESIGN INCORPORATE BIOLOGICAL TRAITS?

During the initial screening of a candidate area for conservation, biological traits can clarify the biological structure and ecology of populations, communities, and ecosystem functions of the area and how these link to environmental and anthropogenic factors. After the appropriate selection of traits and the collection of information on trait expressions in the taxa or individuals sampled to create a list of trait expressions in the area, application of the methodology of choice follows (e.g., biological trait analysis or a similar approach, and/or the use of trait-based functional diversity indices). The results can be used to relate trait expression in populations or communities to physical features and threats and to understand differences among contrasting locations in the area and the traits that drive them. Because traits link to functions, these approaches enable linking of communities to ecosystem processes and building of maps of ecosystem functioning.

Based on the information gathered during the screening process, managers can then identify priorities and objectives for conservation, plan area boundaries, and define regulations. Biological traits can facilitate this phase by providing information on species or community vulnerability, important functions expressed (e.g., which functions to protect in the area and which processes are more vulnerable to threats), and the traits related to these questions (e.g., which traits provide those functions and which traits express vulnerability to threats). Boundaries and protection levels can then be set by using traits to identify areas in the region where important or vulnerable traits occur most often or need protection. Monitoring protocols that investigate whether the management achieves its objectives can also use traits (e.g., whether the intervention preserved or restored important traits over time).

on biological communities (Bremner et al. 2006b, Lefcheck et al. 2015, Nock et al. 2016). Considering multiple traits leads to a more holistic representation of functional diversity, including both the tracking and prediction of trait responses of organisms and communities to different scenarios and changes (Lefcheck et al. 2015). This benefit is particularly relevant for large-scale investigations, where a variety of factors typically affect traits (Lefcheck et al. 2015). Different traits may also drive different ecosystem processes, including potentially unidentified functions (Petchey & Gaston 2006). Managing biodiversity based on multitrait diversity indices produces an inclusive framework that aims to support multiple ecosystem functions and associated goods and services (de Bello et al. 2010, Lefcheck et al. 2015). However, redundant traits should be avoided because similar traits add no new information and can combine to empirically overcontribute to diversity indices, hence disguising functional diversity effects (Nock et al. 2016). Ultimately, the selection of biological traits for analysis should be based on a trade-off between the information each trait provides and the time and effort required to gather such information (Bremner et al. 2006b).

Third, analyses should include intraspecific trait variability, if such an approach is warranted and possible. This goal may be achieved by measuring and including individual trait expressions in the analysis of the population considered and applying methodologies that incorporate intraspecific trait variability (e.g., as proposed in de Bello et al. 2011). This need is particularly important for species whose traits vary considerably within or across populations and especially when management assessments span large scales, such as regional fishing assessments. Sometimes assessment of functional aspects of biodiversity can occur without assessing taxonomical diversity first. Some easily measured morphological traits (such as those for sponge or coral reefs, where taxa are hard to distinguish but morphological features relate directly to habitat complexity) can provide a relatively inexpensive and time-saving solution for assessing diversity for conservation purposes (Vandewalle et al. 2010).

Finally, trait and methodology selection should be informative yet relatively simple to measure and interpret. The selection of traits and analytical tools should balance the sensitivity

and power of the tool to describe assemblages, functions, and responses to impacts with the ease with which traits can be measured and results can be interpreted (Bremner et al. 2006b, Lefcheck et al. 2015). Thus, while we advocate for considering individual variability in traits and including as many taxa and traits as possible, analyses, by necessity, may need to focus on a subset of the available data, such as the most abundant or widespread species (Bremner 2008). Moreover, indicators should also be appropriate for comparative studies across different communities, habitats, and ecoregions to enable applications in future monitoring protocols and comparisons with other locations (Vandewalle et al. 2010). Ultimately, establishing standardized methodologies for trait parameterization will offer a more accessible tool kit to advance marine conservation.

CONCLUSION

Trait-based indicators can complement, rather than replace, traditional biodiversity and habitat-based indicators in marine conservation. The specific added benefits include (*a*) identifying priorities for conservation by assessing and predicting the sensitivity and vulnerability of communities to anthropogenic impacts and climate change, predicting species extinction risk, and assessing community resilience; (*b*) implementing spatial planning by identifying new hot spots of diversity, identifying hot spots of function, and creating maps of functional diversity and functioning; and (*c*) informing monitoring programs that are designed to detect early recoveries after PA establishment and create functional diversity time series (**Figure 1**). For example, trait-based approaches allow the identification of species responsible for key ecological processes, tracing function-related changes back to changes in the biota and hence back to impacting activities that management measures can control (Frid et al. 2008). Thus, trait-based approaches add a fundamental aspect to toolboxes available for conservation efforts and merit consideration in management decisions on ocean sustainability strategies. Such approaches can be relatively easy to estimate once they have been defined and standard methodologies have been established (Hodgson et al. 2005), and they therefore offer an excellent tool for managers (Vandewalle et al. 2010). However, advances in knowledge of marine species traits and how they respond to stressors and link to changes in ecosystem functions point to the need for ongoing development of pragmatic tools to apply trait-based approaches in marine conservation.

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Contents

Errata

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