



# Traits Shared by Marine Megafauna and Their Relationships With Ecosystem Functions and Services

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Traditional ecological research has focused on taxonomic units to better understand the role of organisms in marine ecosystems. This approach has significantly contributed to our understanding of how species interact with each other and with the physical environment and has led to relevant site-specific conservation strategies. However, this taxonomic-based approach can limit a mechanistic understanding of how environmental change affects marine megafauna, here defined as large fishes (e.g., shark, tuna, and billfishes), sea turtles, marine mammals, and seabirds. Alternatively, an approach based on traits, i.e., measurable behavioral, physiological, or morphological characteristics of organisms, can shed new light on the processes influencing structure and functions of biological communities. Here we review 33 traits that are measurable and comparable among marine megafauna. The variability of these traits within the organisms considered controls functions mainly related to nutrient storage and transport, trophic-dynamic regulations of populations, and community shaping. To estimate the contributions of marine megafauna to ecosystem functions and services, traits can be quantified categorically or over a continuous scale, but the latter is preferred to make comparisons across groups. We argue that the most relevant traits to comparatively study marine megafauna groups are body size, body mass, dietary preference, feeding strategy, metabolic rate, and dispersal capacity. These traits can be used in combination with information on population abundances to predict how changes in the environment can affect community structure, ecosystem functioning, and ecosystem services.

**Keywords:** body size, cetacean, dietary preference, fish, seabird, sea turtle

## USING ORGANISMAL TRAITS TO INVESTIGATE ECOLOGICAL PATTERNS

Most of the traditional research on the conservation of biological diversity focuses on species identities and on how their numbers and abundances change in space and time (Rosenzweig, 1995). Observations on biodiversity and ecosystem functioning relationships suggest, for example, that as species richness increases, the productivity and stability of communities also increase (Tilman, 2001; Tilman et al., 2014). It has been argued, however, that a focus on taxonomic units (e.g., species or genus) alone is not sufficient to predict the effects of environmental change on

biological communities and their ecosystem functions (Díaz and Cabido, 2001; McGill et al., 2006; Violle et al., 2007). Species that go extinct can be replaced by species with similar traits and functions (Violle et al., 2014), and intraspecific trait variability (i.e., variability among individuals due to phenotypic plasticity or genetic differences) can be as broad as trait variations across species (Des Roches et al., 2017; Messier et al., 2010; Violle et al., 2012).

A trait-based perspective to community ecology thus resurfaced as a potential approach to enhance our mechanistic understanding of how structure and functions of communities vary along environmental gradients (McGill et al., 2006). Central to this perspective are traits, which are morphological, physiological, or behavioral features of organisms that can be quantified at different organizational levels, from individuals to ecosystems (McGill et al., 2006; Violle et al., 2007). Changes in habitat can strongly affect trait distributions and coexistence because organisms sharing traits that favor habitat occupancy are likely to persist in a given community, whereas those with poorly adapted traits are likely to disappear (Luck et al., 2013). Thus, traits can help us understand and quantify niche occupancy (Violle et al., 2007). Also, the traits that define the fitness of organisms are closely related to ecosystem functions. For example, a seabird behavioral trait such as migration ability can be related to functions like nutrient transport (Doughty et al., 2016).

Trait-based approaches are being promoted for studying community structure and functions of various groups of organisms, including terrestrial plants (Kattge et al., 2011; Kraft et al., 2015), phytoplankton (Litchman and Klausmeier, 2008; Acevedo-Trejos et al., 2018), zooplankton (Litchman et al., 2013) corals (Madin et al., 2016), mammals (Jones et al., 2009), fishes (Stuart-Smith et al., 2013; Ladds et al., 2018), and microbes (Krause et al., 2014). This approach is also fostering global collaborative efforts through the establishment of open trait databases (Jones et al., 2009; Kattge et al., 2011; Parr et al., 2014; Wilman et al., 2014; Kremer et al., 2017). However, the lack of a consistent trait-based framework for the study of marine megafauna, here comprising large fishes (e.g., billfishes, tuna, and sharks), sea turtles, marine mammals (i.e., pinnipeds, sirenians, and cetaceans) and seabirds, prevents a mechanistic understanding of the effects that changes in diversity can have on ecosystem functioning, a challenge still difficult to address for many aquatic communities (Meunier et al., 2017; Degen et al., 2018). Also, marine megafauna has been largely affected by mortality related to bycatch, various forms of pollution, overfishing, habitat degradation, and climate variability, problems that are causing population declines and loss of functional diversity at a global scale (Croxall et al., 2012; Albouy et al., 2017; Pimiento et al., 2017). Finally, the decline of populations within marine megafauna communities can reduce functional diversity, but the impacts on ecosystem functioning are far from being understood (Naeem et al., 2012; Lynam et al., 2017).

Here we list, categorize and describe relevant traits shared by communities of large fishes, sea turtles, marine mammals, and seabirds to guide further investigations and comparisons over

these organisms. We then highlight the relationships between these traits and ecosystem functions and services relevant for studying the community ecology and the conservation of marine megafauna.

## LITERATURE REVIEW

We listed traits of marine megafauna and the associated ecosystem functions and services based on a systematic review of scientific articles published over the last 15 years and up to March 2018. We performed the literature search in Web of Science for the terms: (1) seabird + trait; (2) marine mammal + trait; (3) dolphin + trait; (4) whale + trait; (5) seal + trait; (6) sirenian + trait; (7) manatee + trait; (8) sea turtle + trait; (9) fish + trait; (10) shark + trait; and (11) marine megafauna + trait. From the resulting list of articles, we selected those that clearly dealt with traits of marine megafauna. After an initial screening of potential traits, we defined the traits terminology based on specialized literature (Spitz et al., 2014; Costello et al., 2015; Albouy et al., 2017; Beauchard et al., 2017; Ladds et al., 2018).

## DEFINING TRAITS, ECOSYSTEM FUNCTIONS, AND SERVICES

Traits of marine megafauna are measurable behavioral, physiological, or morphological characteristics of sea turtles, large fishes, marine mammals, and seabirds. Functional traits are those that can affect the performance of organisms and their ecosystem functions (McGill et al., 2006). Examples include body mass, locomotion mode, feeding strategy, and life span. Functional diversity comprises the diversity of functional traits (Mason and Mouillot, 2013). Ecosystem functions encompass vital activities of organisms, including feeding, growing, moving, and excreting, and influence ecosystem functioning (DeLaplante and Picasso, 2011). Ecosystem services are defined as functions that provide goods to humans (Costanza et al., 1997; Cardinale et al., 2012; Mace et al., 2012).

## TRAITS SHARED BY LARGE FISHES, SEA TURTLES, MARINE MAMMALS, AND SEABIRDS

We identified a total of 33 traits that can be measured and used comparably over sea turtles, large fishes, marine mammals, and seabirds (Table 1). These traits are classified into conceptual categories related to morphology, behavior, demography, physiology, biogeochemical composition, and socioeconomic importance. Characteristics such as taxonomic family, common names, IUCN threat categories can be also found in the literature (e.g., Costello et al., 2015), but were not considered here since they are derived from other traits and constitute imprecise or redundant information. We also did not consider traits related to the size of body parts because they typically scale with body size, and a number of them are

**TABLE 1** | Summary of traits of marine megafauna and the related ecosystem functions and services.

Trait type	Trait	Description	Functions	Services	Example
M	Body size	Total length in cm, or m.	Nutrient storage and transport.	Nutrient cycling, promotion of biological diversity, and food provision.	(Andersen et al., 2016; Beauchard et al., 2017)
M	Body mass	Total weight in g or kg.	Nutrient storage and transport.	Nutrient cycling, promotion of genetic diversity, and food provision.	(Andersen et al., 2016; Blanchard et al., 2017)
M	Body condition	Body condition indexes (e.g., kg/m).	Nutrient storage and transport.	Nutrient cycling, and promotion of biological diversity.	(Jenouvrier et al., 2015)
B	Migration	Distance traveled per day, year, or month; or with categories, e.g., resident or migratory.	Nutrient transport, and community shaping through organism dispersal.	Support of trophic state in low productive areas, biodiversity promoting, and maintenance of genetic diversity.	(Doughty et al., 2016)
B	Dispersal performance	Speed of locomotion (km/h) or trip duration (h/day).	Nutrient transport, and community shaping through organism dispersal.	Support of trophic state in low productive areas, biodiversity promoting, and maintenance of genetic diversity.	(Cavallo et al., 2015; Jenouvrier et al., 2015)
D	Mortality rate	Number of deaths per unit of time.	Nutrient transport, and soil fertilization via carcass decomposition.	Support of trophic state in low productive areas, biodiversity promoting, maintenance of genetic diversity, and soil fertility.	(Foote, 2008; Robeck et al., 2015)
D	Fecundity	Number of eggs or neonates per reproductive season.	Nutrient storage.	Nutrient cycling, and food provision, in case of sustainable harvest by traditional societies.	(Abadi et al., 2017)
D	Incubation time	Time in days.	Nutrient storage.	Nutrient cycling, maintenance of trophic interactions and ecosystem stability.	(Cavallo et al., 2015)
D	Life-span	Time in years.	Nutrient storage.	Nutrient cycling, maintenance of trophic interactions and ecosystem stability.	(Plot et al., 2012)
D	Life stage	Age measured in years or categories, e.g., juveniles and adults.	Nutrient storage, trophic-dynamic regulations of populations, and biodiversity promotion.	Nutrient cycling, maintenance of trophic interactions, biological control and ecosystem stability.	(Putman et al., 2018)
D	Reproductive success	The number of offspring per breeding attempt or lifetime.	Nutrient storage.	Nutrient cycling, maintenance of trophic interactions and ecosystem stability.	(Fay et al., 2018; Lowther and Goldsworthy, 2011)
D	Survival rate	The number of individuals per period season or year.	Nutrient storage and transport, and soil fertilization via carcass decomposition.	Nutrient cycling, support of trophic state in low productive areas, and promotion of biological diversity.	(Szostek and Becker, 2015; Abadi et al., 2017)
D	Recruitment age	The proportion of recruitment age in relation to the lifetime.	Nutrient storage.	Biodiversity promoting.	(Fay et al., 2017)
D	Reproductive location	Multiple categories, e.g., beach, water column, rocks, and trees.	Nutrient storage and soil fertilization associated to excretion.	Biodiversity promotion, maintenance of genetic diversity, and soil fertility.	(Costello et al., 2015)
D, B	Sociability	Number of individuals per group or flock.	Nutrient storage, ecosystem engineering via bioturbation, soil fertilization via excretion and community shaping by altering primary productivity.	Biodiversity promotion, maintenance of genetic diversity and ecosystem stability, and soil fertility.	(Costello et al., 2015; Durrett et al., 2014)
B	Food intake rate	The amount of prey or other resource, e.g., fish, milk, and ingested per unit of time.	Trophic-dynamic regulations of populations, community shaping and nutrient storage.	Biological control of pests and invasive species, and maintenance of trophic interactions and ecosystem stability.	(McDonald et al., 2012; Beauchard et al., 2017)

*(Continued)*

TABLE 1 | Continued

Trait type	Trait	Description	Functions	Services	Example
B	Dietary preference	Categories: omnivore, planktivorous, carnivore, herbivorous or scavenger, which can be organized in ordinal scale, or relative importance (%), or prey groups.	Nutrient storage and trophic-dynamic regulations of populations.	Biological control of pests and invasive species, nutrient cycling, maintenance of trophic interactions, and proxy for fishery targets.	(Wilman et al., 2014; Houle et al., 2016)
B	Prey-predator mass ratio	The mass of the prey divided by the mass of the predator.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, biological control, and maintenance of trophic interactions and ecosystem stability.	(Carbone et al., 2014)
M, B	Optimal prey size	Averaged size of the prey.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, biological control, and maintenance of trophic interactions and ecosystem stability.	(Houle et al., 2016; Blanchard et al., 2017)
B	Feeding strategy	Multiple categories: benthic-feeding, pelagic-feeding, surface-feeding, or more specific; or organized in ordinal scale.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, biological control of pests and invasive species.	(Paredes et al., 2015)
B	Feeding distance	Distance between the breeding location and foraging area.	Nutrient storage, community shaping via organism dispersal.	Nutrient cycling and promotion (or maintenance) of biological diversity.	(Copello et al., 2016)
B	Dive depth	The diving depth in meters.	Nutrient storage, nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, promotion (or maintenance) of biological diversity, and biological control.	(Grémillet et al., 2012; Spitz et al., 2014)
B	Dive duration	The amount of time spent on each diving, per unit of time.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, promotion (or maintenance) of biological diversity, and biological control.	(Hassrick et al., 2013; Ciancio et al., 2016)
B	Foraging depth	The foraging depth in meters.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, promotion (or maintenance) of biological diversity, and biological control.	(Young et al., 2010; Ceia and Ramos, 2015)
B	Dive profile	Dive depth divided per dive duration, or frequency of undulation (substantial changes in depth, e.g., >0.3 m) during diving.	Nutrient storage and trophic-dynamic regulations of populations.	Nutrient cycling, and promotion (or maintenance) of biological diversity.	(Simeone and Wilson, 2003; Gleiss et al., 2011; Meir et al., 2013)
B	Defense mechanism	Mechanism to reduce predation/parasitism: behavioral (e.g., complex nest building), morphological (e.g., turtle shell), chemical (e.g., bird odorants against parasites).	Nutrient storage.	Nutrient cycling, and promotion of biological diversity.	(Douglas et al., 2004)
P	Temperature preference	The optimum habitat temperature selected by most of individuals, or body temperature.	Nutrient storage.	Nutrient cycling, and promotion of biological diversity.	(Grémillet et al., 2012; Cavallo et al., 2015)
P	Metabolic rate	The oxygen consumption per unit of time (e.g., ml/min).	Nutrient storage and trophic-dynamic regulations of populations.	Biological control of pests and invasive species, nutrient cycling, and promotion of biological diversity.	(Teixeira et al., 2014)
P	Growth rate	The weight or length gained per unit of time (e.g., g/day).	Nutrient storage.	Nutrient cycling, and promotion of biological diversity.	(Amano et al., 2014)
P	Excretion rate	The amount of excreted material per unit of time (g/day).	Nutrient storage, soil fertilization via excretion, and community shaping by altering primary productivity.	Nutrient cycling, promotion of biological, and soil fertility.	(Hilton et al., 2000, 2008)

(Continued)

TABLE 1 | Continued

Trait type	Trait	Description	Functions	Services	Example
BG	Nutrient composition	The mean amount of nutrients per individual, or stoichiometric ratios.	Nutrient storage and transport, and soil fertilization.	Nutrient cycling, support of trophic state in low productive areas, and promotion of biological diversity.	(Louzao et al., 2008)
P	Prey sensing	The way organisms locate prey: mechanosensing, visually, chemosensing, or echolocation.	Nutrient storage and trophic-dynamic regulations of populations.	Biological control of pests and invasive species, and maintenance of trophic interactions and ecosystem stability.	(Friesen et al., 2017)
S	Charismatic potential	Low, medium, or high potential for attracting tourists, measured in ordinal scale, or the estimated annual income in a given region generated by tourists attracted by organisms.	Recreation and cultural.	Providing opportunities for recreational activities.	(Daniel et al., 2012)

Trait types include: morphological (M), demographical (D), behavioral (B), physiological (P), biogeochemical (BG), and socioeconomic (S). Functions and services are classified according to scientific literature (following the criteria of Costanza et al., 1997; de Groot et al., 2002; Hattam et al., 2015). Example includes at least one reference reporting on the trait listed. This list highlights associations between traits, functions and services, but different associations can be considered depending on the perspective of a given study.

not comparable (or display different functions) across different groups of marine megafauna (e.g., bill culmen, toes, size of legs, dorsal, and caudal fins). Furthermore, a trait such as diving depth can be quantified in many ways, including, for example, minimum, maximum, or average diving depth, but to avoid redundancy, here we considered average diving depth, diving duration, and diving profile (Gleiss et al., 2011; Meir et al., 2013; Ciancio et al., 2016).

Due to allometric effects, body size and body mass constitute key traits because they are correlated with many other morphological, physiological, and behavioral characteristics. Size of jaws, mobility, feeding distance, incubation time, life-span, recruiting rate, growth, metabolic rate, and excretion rate all scale with body size and body mass (Schreiber and Burger, 2002; Louzao et al., 2008; Froy and Richard, 2013; Fraija-Fernández et al., 2015; Nunes et al., 2017). This property makes body size useful for reducing the dimensionality of the broad trait space. Body size also holds the potential to describe marine life from bacteria to whales, to help overcome some of the limitations inherent to taxonomic-based studies, and to understand variability in functional diversity over very distinct classes of organisms and environmental gradients (Andersen et al., 2016; Blanchard et al., 2017). Body size and body mass are also very useful to predict organismal vital functions (e.g., metabolic rates: West et al., 2002), and their contributions to ecosystem functioning.

Metabolic theory predicts how body size scales with metabolic rate (Brown et al., 2004). However, variability can be observed across different groups of marine megafauna, due to differences in diet composition (Jobling, 1981; Lutcavage and Lutz, 1986; McNab, 1988; Williams et al., 2001). Carnivore killer whales *Orcinus orca* display metabolic rates of 20–30 mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>, substantially higher than filter-feeding sharks of similar sizes, such as the basking shark *Cetorhinus maximus* which the metabolic rate is estimated at around 0.01 mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup> (Sims, 2000; Guinet et al., 2007). For example, the carnivorous

bottlenose dolphin *Tursiops truncatus* can exhibit a basal metabolic rate (10.12 mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>), which is two times higher than the one of the omnivorous leatherback sea turtle *Dermochelys coriacea* (4.77 mL O<sub>2</sub> kg<sup>-1</sup> min<sup>-1</sup>), although they both have similar body size and mass (Lutcavage and Lutz, 1986; Williams et al., 2001). Also, sea turtles feed by pursuing preys through the water column and low metabolic rates are a consequence of the long dives and of the fact that increased metabolic rates in ectoderms impose energetic imbalances (Butler et al., 1984; Lutz and Musick, 1996; Fossette et al., 2012). To better predict the effects of organisms on ecosystem functions and services, body size should, therefore, be used in combination with traits that shape the fundamental ecology of marine megafauna, including thermal tolerance (Pimiento et al., 2017), metabolic and food intakes rates (Woodward et al., 2005), and dietary preference (Houle et al., 2016).

Phenotypic trait variation within species (intraspecific variation) can be as broad as trait variation across species of fishes, sea turtles, marine mammals, and birds (Albert et al., 2010; McClain et al., 2015; Samarra et al., 2017). Total length in basking sharks, for example, ranges between 1.5 and 10 m (McClain et al., 2015). However, food web models usually rely on the biomass of organisms, which is inferred using values of body mass averaged within species level (Costa et al., 2017). This approach may overlook a substantial variation in body mass across individuals of the same species. Finding new approaches for addressing intraspecific variations in food web models can lead to improved predictions of nutrient and energy fluxes via trophic interactions and ecosystem stability. Efforts are being made to build databases that includes trait values within species of marine megafauna (Petchey et al., 2008; Wilman et al., 2014; McClain et al., 2015; Des Roches et al., 2017), but information on intraspecific trait variation is fragmented and species-specific.

A large body of research on the trait ecology of marine megafauna is based on categorical traits because these properties are straightforward to measure (Costello et al., 2015;



Albouy et al., 2017). However, the qualitative nature of categorical traits can limit comparisons between different groups of organisms (McGill et al., 2006). Regarding the level of sociability, for example, an organism can be classified as gregarious, colonial, solitary, or even in intermediary categories (Costello et al., 2015). For sharks, dolphins, and whales, the term gregarious can refer to small groups of 5 to 200 individuals (Mann et al., 2000; Baird, 2009; Crowe et al., 2018), but for colonial seabirds, the term refers to thousands of individuals (Schreiber and Burger, 2002; Jovani et al., 2008). Alternatively, traits estimated quantitatively can be standardized and compared across different groups of organisms, and potential trade-offs can be explored (Genovart et al., 2013; Shoji et al., 2015; Gravel et al., 2016; Yamamoto et al., 2016). Some traits, such as body size, can be easily quantified, but others cannot. Preferred diet, for example, is largely treated as a categorical trait and categories usually include zooplankton, invertebrate, and fish (Albouy et al., 2017). Categories of food items can be standardized into semiquantitative information by considering their relative importance (Wilman et al., 2014). Furthermore, an increasing amount of numerical data for dozens of megafauna species can be freely downloaded from the COMADRE Animal Matrix Database<sup>1</sup>. Compiled information on morphological, behavioral, physiological, and demographical traits of marine megafauna can also be easily found in specialized books providing ground knowledge on the natural history of these organisms (Schreiber and Burger, 2002; Spotila, 2004; Jefferson et al., 2015).

## LINKING TRAITS TO ECOSYSTEM FUNCTIONS AND SERVICES

The traits shared by marine megafauna are mainly related to ecosystem functions including nutrient storage, trophic-dynamic regulations of populations, community shaping, and habitat provision (Table 1). Also, almost all traits can be linked to nutrient storage and cycling (Table 1). Although we made a number of suggestions on how to link traits with ecosystem functions and services, establishing relationships between these properties broadly depends on the perspective of a given study. For example, food intake rate and dietary preference are intrinsically related to trophic-dynamic regulations of populations of specific taxa (Levin et al., 2001; Myers et al., 2007; Costa et al., 2017), but these traits can be also related to nutrient storage, because nutrients are transferred from the consumed to the consumer (Roman et al., 2014). Organismal dispersal performance and sociability are associated with soil fertilization via excretion (Zwolicki et al., 2013; Doughty et al., 2016), and can be related to nutrient storage by changes in primary production (Table 1). Especially body size and body mass correlate with a large number of traits and can serve as a master trait to investigate the drivers of various ecosystem functions and services (Figures 1A,B). Food intake rate, for example, varies according to body size and is related to trophic-dynamic regulations of populations and community structure

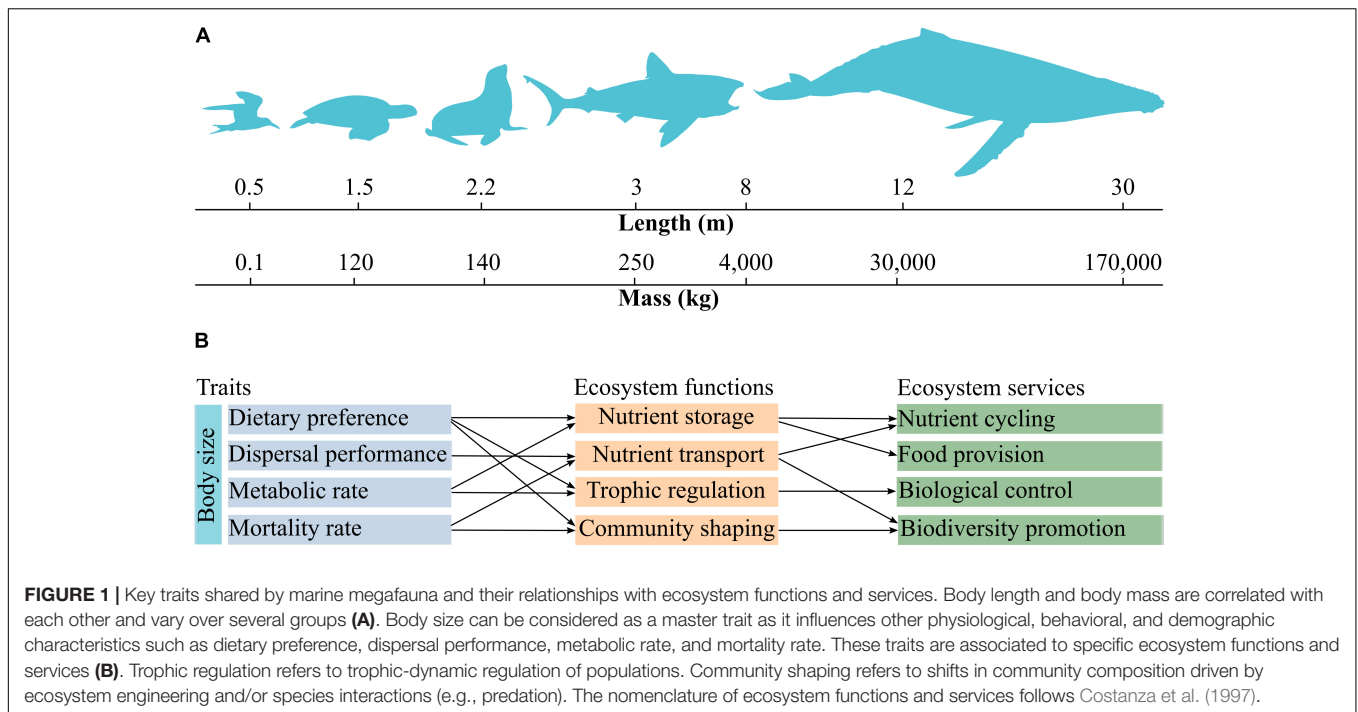
since it regulates the abundance of specific prey taxa (Thomsen and Green, 2016; Figure 1B). Food intake rate can be linked to nutrient storage and cycling because it reflects nutrient flows via trophic interactions. Also, the almost ubiquitous association of nutrient storage with different traits and functions results from fundamental interactions among and between organisms and their environment, which in turn influences food chain length, trophic biomass, and nutrient cycling at a planetary scale (Loreau, 1995; Leroux et al., 2012).

Nutrient storage, which is closely related to the contribution of marine megafauna to nutrient cycling, is also fundamentally related to food production, the latter being an essential ecosystem service for human well-being (Pauly and Christensen, 1995; Costanza et al., 1997). Nutrient storage, converted to food source for humans by means of fishing or aquaculture production, had intensified over past half-century leading to overexploitation of various populations of marine megafauna (Pauly et al., 2002; Springer et al., 2003). Body size, in combination with population abundances is highly associated to food production because fishing methods typically select for larger piscivorous organisms (e.g., haddocks, bonitos, rays, billfishes, tunas, sharks, and marine mammals), which have higher nutritional and economic value (Pauly and Christensen, 1995; Clements et al., 2017). However, as larger fishes get scarcer, fishing targets shift to smaller planktivorous fishes and invertebrates (Pauly, 1998; Pauly et al., 2002). This shift has been altering the structure of marine food webs, and posing a risk not only to global biodiversity, but also to food production (Springer et al., 2003; Worm et al., 2006; Butchart et al., 2010).

Large fishes, sea turtles, marine mammals, and seabirds are particularly important for the biogeochemical cycle of major elements because they are widespread, display high mobility, and are abundant worldwide (Speakman, 2005; Wing et al., 2014). Body size, is one of the most crucial traits related to nutrient transport because bigger animals hold more nutrients and feature impressive dispersal capacities (Andersen et al., 2016; Doughty et al., 2016; See Figure 1). For example, a 15 m long humpback whale *Megaptera novaeangliae* weighs ca. 35,000 kg (Lockyer, 1976), which is thousands times heavier than seabirds such as the Manx shearwater *Puffinus puffinus*, which has an average size of 0.34 m and a weight 0.46 kg (Schreiber and Burger, 2002). However, the global population of shearwaters (790,000 individuals) is 13 times larger than that of humpback whales (about 60,000 individuals), thus making the contribution of seabirds to nutrient cycling also quite important. Combining body size and population abundances is thus crucial for understanding the contribution of different marine megafauna communities to nutrient storage and cycling. This is particularly relevant because the capacity of marine megafauna to transfer nutrients across land and ocean decreased by 6% of its global natural capacity due to population declines (Doughty et al., 2016). Global seabird populations, for example, have declined by almost 70% over the last 50 years (Paleczny et al., 2015), with unknown impacts on nutrient storage and transport worldwide.

Information on population abundances is often valuable to trait-based approaches since the number of organisms can

<sup>1</sup><http://www.compadre-db.org/>



affect the variability and dominance of traits within biological communities. For example, whaling activities during the first half of the nineteenth century have reduced the population of blue whales *Balaenoptera musculus* in the southern hemisphere to about 1% (Christensen, 2006), with only a slow recovery being forecasted in the next decades (Tulloch et al., 2017). The dramatic population decline of these large whales provoked an excess in krill availability, which not only reshaped the krill community but also increased the populations of other smaller vertebrates, such as mink whales *B. acutorostrata*, penguins, and various pinnipeds (Estes, 2009; Roman et al., 2014). The current population of Caribbean green sea turtles is 3–7% the size of the population prior to the exploitation period, i.e., by about 1800, when turtles and their eggs were intensively and persistently harvested (Jackson, 1997, 2001). The decrease in the number of sea turtles triggered an expansion of their main food source, the seagrass *Thalassia testudinum*, which, in turn, caused an increase in the density of epibiont. These changes facilitated the deposition of the substrate and the colonization for diverse species of invertebrates and fishes (Bjorndal and Jackson, 2003). Compared to sharks, dolphins and whales, seabirds are relatively small, but with larger population sizes they can shape biological communities by transferring matter between distant areas via nutrient uptake, excretion, and carcass deposition (Polis and Hurd, 1996). Soils hosting large colonies of seabirds, such as blue-footed boobies *Sula nebouxii* show very high concentrations of ammonium and phosphate, which favors the establishment of creeping vegetation and the associated invertebrates (Havik et al., 2014; Lynam et al., 2017; Graham et al., 2018). However, the impact of seabird population declines on biological communities associated to breeding colonies is still limited. To investigate the contribution of megafauna to

community structure, population abundance can be used in combination with other traits related to nutrient storage and nutrient cycling, such as excretion rate, reproductive location, and level of sociability.

Marine megafauna includes large, widespread and easily observable organisms displaying a set of traits appreciated by humans. These organisms are thus among the most charismatic in the world (Albert et al., 2018). Charismatic potential can be considered as trait contingent on human (or societal) perception with a strong association to recreational and cultural ecosystem services (Costanza et al., 1997). Such trait leads to services that provide economical (tourism) or cultural (aesthetic) benefits. The economical revenues derived by such services can, in turn, help to mitigate the negative impacts of biodiversity loss (Costanza et al., 1997; Whelan et al., 2015; Table 1). For example, whale watching generates an income of 10 billion US \$ per year worldwide, and national parks in the United States and Germany earn, respectively 10 billion US \$ and 500 million € per year (Mayer et al., 2010; Daniel et al., 2012). These activities provide a wealth and an environmental awareness that can indirectly influence other ecosystem functions and services.

## FUTURE PERSPECTIVE

Trait-based approaches can help us to understand how the structure of marine megafauna communities re-organize under environmental change and adverse conditions, including habitat loss, increasing pollution, and disease spreading (Keesing et al., 2010; Cardinale et al., 2012; Pimiento et al., 2017). A relatively unexplored avenue of research in the ecology of marine megafauna is the use of trait-based approaches to

elucidate the importance of functional diversity, an essential component of overall biodiversity (Tilman, 2001). This field of research can provide valuable insights into the mechanisms shaping the patterns of megafaunal trait diversity and ecosystem function relationships.

One of the most significant quests in ecology today is to understand the impacts of plastic pollution on populations of marine megafauna. Evidence is accumulating about the ingestion of plastic by fishes, sea turtles, seabirds, and marine mammals (Schuyler et al., 2016; Lynam et al., 2017; Tavares et al., 2017). Plastics are also abundant in nests of some seabirds, such as the brown boobies *S. leucogaster*, with unknown consequences to chickens and the quality of breeding habitats (Grant et al., 2018; Battisti et al., 2019). Future research should concentrate efforts on investigating which type of traits are most closely related to plastic accumulation among marine vertebrates. Feeding strategy and depth, for example, may play an important role in relation to plastic ingestion (Tavares et al., 2017).

Information on the frequency and number of individuals stranded among sea turtles, pinnipeds, cetaceans, and seabirds has been used recently to quantify mortality patterns (Moura et al., 2016; Tavares et al., 2016; Flint et al., 2017). Carcasses found washed onshore can be collected easily and with low costs, and constitute a convenient source of information for assessing the distribution and variability of morphological, physiological, and demographical traits in relation to local environmental stressors (Spitz et al., 2006; Thompson et al., 2013; Amano et al., 2014; Fruet et al., 2015). This approach is particularly useful for species that are rare and difficult to observe, such as melon-headed whales *Peponocephala electra* (Amano et al., 2014). Examining stranded carcasses is also a non-invasive way of measuring traits in species with critical conservation status and in declining populations, such as the white-chinned petrel *Procellaria aequinoctialis* (Cipro et al., 2013).

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Measuring traits of marine megafauna can be a challenging task. In contrast to plants, coral reefs, plankton, and invertebrates, marine megafauna is highly mobile and hard to capture. For example, some rare and cryptic marine mammals, such as the dwarf sperm whale *Kogia sima* and the franciscana dolphin *Pontoporia blainvillei* are difficult to detect in the field (Moura et al., 2009; Hodge et al., 2018). For these types of organisms, it is challenging, if not impossible, to measure traits such as food intake rate and metabolic rate. Hence, body size and body mass are particularly valuable as they can be precisely quantified and correlated with other traits at different levels of organization, from individuals to communities.

## AUTHOR CONTRIBUTIONS

DT, EA-T, JdM, and AM conceived the study. DT, JdM, and EA-T revised the literature. DT built the table of traits. DT wrote the manuscript. AM, EA-T, and JdM assisted with writing and discussed the contents.

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**Conflict of Interest Statement:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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