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# Energyscapes pinpoint marine megafauna feeding hotspots in the Mediterranean

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Affiliations are included on p. 10.

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Ocean giants shape the structure and functioning of marine food webs via trophic top–down controls, landscapes of fear, vertical and horizontal redistribution of nutrients, energy, and matter. Yet, they face threats from overfishing, pollution, habitat degradation, and climate change, and one-third of marine megafauna species are at risk of extinction, ultimately endangering the resilience of entire ecosystems. In such a context, knowing when and where megafauna find resources to balance their substantial energy requirements is critical for their management. Through an energyscape approach integrating abundance censuses, diet, and energy requirements, we investigated the prey consumption patterns of Mediterranean marine megafauna during the summer. We thereby shed light on a diverse guild of species composed of fishes, mammals, reptiles, and birds and estimated that 4.1 million individuals consume 1.6 million tons of prey each summer, pelagic cephalopods being the primary food resource and cetaceans and tunas being key players in the community. Spatial patterns in prey consumption reflected the diverse distribution and needs of the megafauna species and underlined the critical importance of the western Mediterranean for the megafauna community. Conservation strategies should prioritize spatial and biological diversity to safeguard megafauna and ecosystem functions across the Mediterranean basin.

energyscape | megafauna | prey consumption | functional ecology | Monte Carlo simulations

The inverted biomass pyramid and the physical properties of the marine realm have led to the evolution of gigantism of top predators across many phylogenetic lineages. Such marine megafauna are not only big, they also have disproportionately large effects on their ecosystem and occupy a central place in marine ecosystems (1, 2). They are a group of highly diverse organisms, with a wide range in body mass, life-history traits, physical characteristics, and contribute to diverse trophic networks, ecosystem structures, and services (1).

Marine megafauna shapes ecosystem structure and function through a variety of processes, such as top–down controls of trophic networks via predation and landscapes of fear, whereby predation risk affects the spatial distribution of potential prey (3–5). These giants also transport and redistribute energy, matter, and nutrients vertically through the water column, by feeding at depth and defecating near the sea surface (1, 2, 6, 7), but also horizontally as they migrate across entire ocean basins, some of them even depositing nutrients on land (seabirds with guano, turtles with eggs; 8).

One-third of marine megafauna species are currently threatened with extinction (9), and given their keystone role in ecosystems, their disappearance may undermine ecosystem resilience, and ultimately that of human societies. Marine megafauna are mostly threatened by anthropogenic impacts, which notably include competition with fisheries, fisheries bycatch, and gear entanglement (10). In addition, ever-increasing maritime traffic impacts this group through collisions, noise pollution, and habitat loss (11, 12), while widespread and diverse plastic and chemical pollution have many negative consequences (13, 14).

Given its geographical location at the crossroads of Africa, Asia, and Europe, the Mediterranean is also one of the most anthropized marine regions on Earth (15), where all of the megafauna-threatening anthropogenic disturbances occur, along with issues of overfishing, marine heatwaves, invasive species, and coastal habitat destruction. Some of these disturbances can reach unique intensity. Notably, 30% of the worldwide marine traffic transits through the Mediterranean (16).

Yet, megafauna are still abundant and diverse in the Mediterranean, which is one of the most biologically diverse parts of the global ocean: While representing only 1% of the

## Significance

The Mediterranean Sea is a biodiversity hotspot, but also the most anthropogenically impacted marine region. Surprisingly, this sea of trouble still harbors a minimum of 4.1 million large fish, mammals, reptiles, and birds. Knowledge of where marine megafauna find the resources to cover their substantial food requirements is important for their effective conservation. Yet, such large-scale assessments of prey consumption are lacking. Using an energyscape approach, we map the megafauna prey consumption over the entire Mediterranean basin. We estimate that the community consumes 1.6 million tons of prey each summer, mostly in the western Mediterranean, and mainly targeting pelagic cephalopods and fish. These results can be used to inform conservation planning for safeguarding Mediterranean ecosystem functions and services.

The authors declare no competing interest.

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world's ocean surface, it hosts ca. 10% of marine species, with an endemism level of 9% (17). For example, the Sea hosts some highly threatened and near-extinct species such as the monk seal *Monachus monachus* and Balearic shearwater *Puffinus mauretanicus*. In a sea where fisheries remove an estimated 1.6 million tons of resources per year (Sea Around Us project; 18), knowing when and where megafauna find enough food resources to balance their substantial energy requirements is critical for their management.

The energy balance of a predator determines the amount, quality, and type of prey it targets (19), and can be used to infer the amount of prey it consumes. This approach has previously been used to assess the competition between fisheries and marine mammals and seabirds, in some oceans and globally (20–24), but has rarely been spatially explicit, never considered the entire megafauna community (fish, mammals, reptiles, and birds), and such analyses have not been conducted across the Mediterranean.

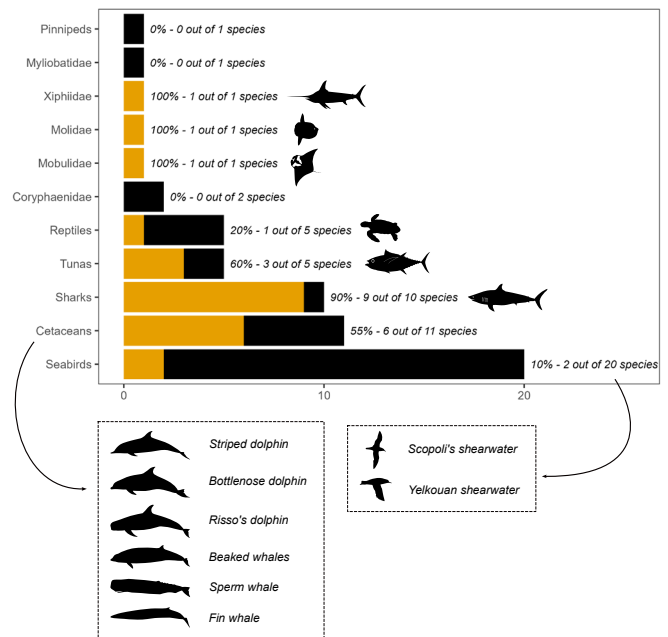
In this context, the energyscape paradigm offers a unique framework to assess marine megafauna feeding seascapes, by describing how the energetic requirements of an animal vary through space and time, according to the intrinsic state of the individual as well as surrounding environmental conditions (25, 26). Here, we set up such a spatially explicit approach describing the spatial distribution of the energetic needs of the majority of Mediterranean megafauna and infer the amount and the spatial distribution of the prey functional groups necessary for the community to meet its needs. This information will ultimately permit tailoring conservation efforts toward habitats and prey most critical for megafauna survival.

## Results

We collated all available information on the spatial distribution and abundance, diet composition, body mass, and energetic needs of Mediterranean pelagic megafauna, and in particular those species that are repeatedly present near the sea surface and/or regularly use the upper water column. We studied 24 out of 58 megafauna species (41%), spanning 8 out of 11 taxonomic groups, including the most abundant species (teleosts, elasmobranchs, cetaceans, turtles, seabirds; Fig. 1A and Table 1). Among them, 16 species are resident to the Mediterranean, six are migrant or occasional visitors and two are of unknown status. For each group, we estimated the energyscape and the foraged biomass consumed during the summer period (June to August) for each prey functional group.

We first reconstructed the body mass distributions based on morphometric information (from stranded, bycaught, or fished individuals), and estimated the field metabolic rate (FMR, the amount of energy necessary for an individual to live; 27) for each species using allometric relationships (Fig. 1B). By scaling FMRs with abundance maps, we described the energyscape of each species across the Mediterranean and coupled this information with the diet composition and the energy content of prey to estimate daily food requirements and the total biomass of prey consumed by each megafauna species in the Mediterranean. Finally, we summarized the spatial distribution of foraged biomass per prey functional group.

Because marine megafauna species are very diversified, both at the intra- and interspecific levels, we used Monte Carlo simulations to propagate the variability associated with each parameter and quantify the species-specific variability of energyscapes and prey biomass consumptions. Thus, all values presented hereafter



**Fig. 1.** Inclusion rate of each pelagic megafauna group of the Mediterranean, contrasting the total number of species present in the basin (bar length) and the number of species considered in the study (gold). Cetaceans and seabirds are split at lower taxonomic levels for further analyses: Cetaceans include striped (*Stenella coeruleoalba*), bottlenose (*Tursiops truncatus*), and Risso's (*Grampus griseus*) dolphins as well as Cuvier's beaked (*Ziphius cavirostris*), sperm (*Physeter macrocephalus*), and fin (*Balaenoptera physalus*) whales, while seabirds include Scopoli's (*Calonectris diomedea*) and yelkouan (*Puffinus yelkouan*) shearwaters. Xiphiidae (swordfish, *Xiphias gladius*), Molidae (sunfish, *Mola mola*), Mobulidae (spine-tailed devil ray, *Mobula mobular*), and reptiles (loggerhead turtles, *Caretta caretta*) are all single-species groups; while tunas and sharks are multispecies groups (see Table 1 for detailed species composition).

are expressed as means and the associated lower 10% and upper 90% bounds of estimated values.

**Individual-Scale Needs.** The species composing the Mediterranean megafauna community have very different individual FMRs (Fig. 2A), ranging from 52 kJ/d [37; 63] for loggerhead turtles to 3.1 million kJ/d [2.8 million; 3.3 million] for fin whales. Overall, cetaceans are the taxonomic group with the highest FMRs, while teleosts (tunas, swordfish) and elasmobranchs (sharks, spine-tailed devil rays) have FMRs similar to those of smaller-sized cetaceans.

Pelagic cephalopods and pelagic and demersal fish are the most commonly eaten prey categories (Fig. 2B). Krill is the sole prey item of fin whales and one of two species eaten by spine-tailed devil rays. Gelatinous prey were consumed mostly by sunfish (considered an obligate gelatinous consumer), but also by sharks and loggerhead turtles, the latter being the only species foraging on benthic and algal resources. Finally, fish larvae, mollusks, and zooplankton are consumed only by tunas, sharks, loggerhead turtles, and yelkouan shearwaters.

Among prey, pelagic fish, demersal fish, and unidentified teleosts have the highest energetic content (Fig. 2C), followed by cephalopods (pelagic, benthic, unidentified). Gelatinous prey items have the lowest energetic content, while krill and other zooplankton are intermediate.

As a result of their different needs and diets, megafauna species have different daily rations, expressed for a single individual and as a proportion of body mass for comparability (Fig. 2D). Fin and sperm whales, although having the largest FMRs, forage on

energy-rich prey species and have efficient lifestyles (low FMR relative to body mass) which results in the species having the lowest mass-specific daily rations, with only 1.9% of body mass [1.4; 2.3] for fin whales, 2.6% [1.8; 3.5] for sperm whales. Spine-tailed devil rays, Cuvier's beaked whales, sharks, tunas, and swordfish each ingest an equivalent of 4% of their body mass per day. Risso's and bottlenose dolphins require slightly higher rations, corresponding to ca. 6% of their body masses (6.3% [4.5; 12.9] and 6.5% [4.0; 8.9], respectively), while striped dolphins have the highest ration among cetaceans (9.4% of their mass [6.5; 12.9]). Loggerhead turtles, Scopoli's shearwaters, and yelkouan shearwaters consume approximately one-fourth of their body mass each day (28.8% [1.6; 53.5], 31.5% [29.8; 33.3], and 24.5% [23.5; 25.6], respectively). Finally, sunfish was the only species consuming more than its body mass each day (198.6% [137.6; 236.8]).

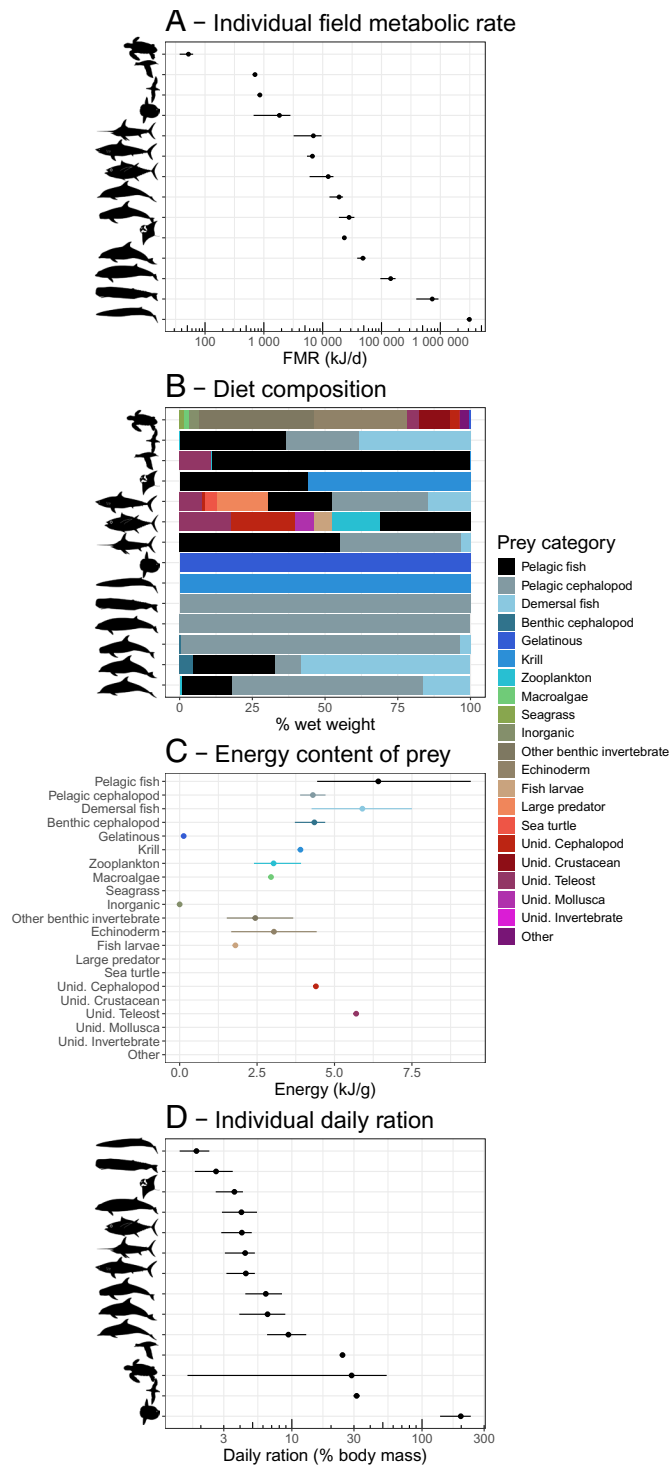
### Population-Scale Needs.

**4.1 million individuals.** The 14 groups of megafauna species account for an estimated 4.1 million individuals (Figs. 3A and 4), of which loggerhead turtle (1,047,700 [713,000; 1,469,000]), tunas (937,000 [167,000; 1,754,000]), striped dolphin (747,000 [390,000; 1,108,000]), and Scopoli's shearwater (654,000 [415,000; 893,000]) are the most abundant, accounting for ca. 82.4% of the total abundance. The least abundant species are the sperm (5,300 [3,300; 7,300]) and fin whales (2,900 [700; 5,200]), contributing only to 0.1% and 0.07% of the total abundance. Most megafauna individuals are distributed in the western Mediterranean Sea (Fig. 3, especially cetaceans, tunas, sunfish, swordfish, spine-tailed devil ray). Large numbers of megafauna individuals also occur east of Tunisia, a pattern mostly driven by the large prevalence of Scopoli's shearwaters and loggerhead turtles.

**0.5 million tons of body mass.** Although the fin whale population accounts for only 0.07% of the total megafauna in terms of the number of individuals, the species is by far the largest with a mean body mass of 55,000 kg. As such, it represents 34.5% of the total biomass of Mediterranean megafauna considered in this study (Fig. 4A). Sperm (13,000 ± 8,000 kg) and Cuvier's beaked (1,500 ± 700 kg) whales contribute significantly to this total biomass, for similar reasons (14.8%, 13.4%, respectively). Tunas account for 15.3% of the megafauna biomass due to the combination of high abundance and high body mass (70 ± 77 kg). On the contrary, the combined populations of sharks (0.6%), sunfish (0.2%), and seabirds (0.01% and 0.08% for Scopoli's and yelkouan shearwaters) represent less than 1% of the total biomass of Mediterranean megafauna.

**53 billion kJ per day.** With average energy requirements of 3.1 million kJ per day for a single individual, the fin whale is a major player within Mediterranean megafauna, with the species accounting for 17.4% of the total energetic needs of those included (Figs. 3B and 4). Yet, because of large population abundances, striped dolphins, tunas and Cuvier's beaked whales are also contributing the most to the total energetic requirements of the community (26.9%, 22.0%, 11.3%, respectively). The least contributing species are Scopoli's shearwater (1%), sharks (0.9%), sunfish (0.3%), yelkouan shearwater (0.2%), and loggerhead turtle (0.1%). As a result of this imbalance, most of the megafauna energetic needs are in the western basin (Fig. 3).

**1.6 million tons of prey consumed per summer.** Cetaceans consume 67.9% of forage resources of Mediterranean marine megafauna (Fig. 4), with 21.6% consumed by striped dolphins (350 thousand tons [120; 610]), 16.6% by fin whales (270

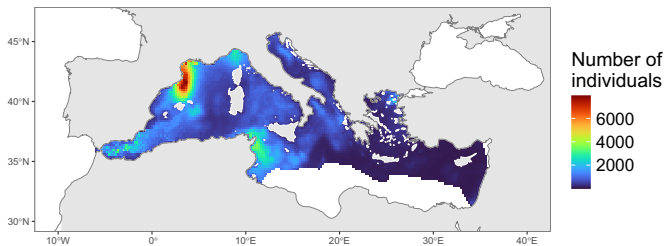


**Fig. 2.** (A) Individual field metabolic rates (FMR) and (B) diet composition (in % of diet wet weight) for the considered megafauna species, (C) energy content of prey functional groups (ordered from the most to least common in megafauna diet) and (D) megafauna individual daily ration expressed as a proportion of body mass. The FMR of Scopoli's shearwater comprises that of all life stages excluding chicks. The prey groups for which no energy content information was available (empty values in panel C) have not been included in further analyses of daily rations and total consumptions.

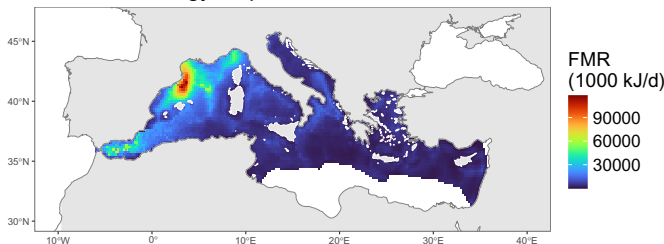
thousand tons of krill [60; 510]), 14.2% by Cuvier's beaked whales (230 thousand tons of pelagic cephalopods [90; 400]), and 10% by sperm whales (161 thousand tons [50; 280] of pelagic cephalopods). Tunas extract 14.9% of all resources



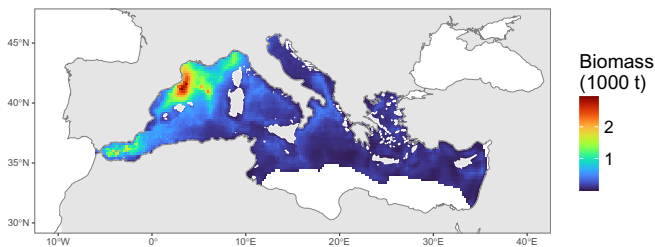
### A – Total abundance



### B – Total energyscape



### C – Total consumed biomass



**Fig. 3.** (A) Total abundance (expressed in number of individuals), (B) total energyscape of Mediterranean marine megafauna, summing all species (expressed in field metabolic rate (FMR) units, kJ per day), and (C) total biomass of forage species consumed by the megafauna community over the course of the summer. The species-specific abundance maps, energyscapes, and consumption maps are presented in *SI Appendix*.

required by the considered megafauna community, with a total of 240 thousand tons of prey taken each summer by this group [21; 560].

Sunfish use 10% of the total consumed biomass, but extract only gelatinous prey (160 thousand tons [41; 321]). Risso's dolphins, bottlenose dolphins, and loggerhead turtles respectively consume 3.0, 2.6, and 2.5% of the total biomass extracted by megafauna in the Mediterranean in the summer, with 50 thousand tons [20; 80] for Risso's dolphins, 40 thousand tons for both bottlenose dolphins ([10; 80]) and loggerhead turtles ([20; 70]). This latter species stands out by foraging on prey not consumed by other predators: Although the largest part of the biomass extracted by loggerhead turtles is gelatinous prey, they also consume 240 tons of echinoderms [90; 440] and 220 tons of other benthic invertebrates [90; 420]. Swordfish consume 30 thousand tons [8; 60] of prey (1.9% of the total), and spine-tailed devil rays 20 thousand tons [10; 40] (1.4% of the total). Sharks (10 thousand tons [0.9; 20]), Scopoli's (10 thousand tons [7; 20]) and yelkouan (1,300 tons [550; 2,000]) shearwaters consume the remaining 1.5%.

Overall, pelagic cephalopods are the most-consumed prey species (Fig. 4), with 740 thousand tons [270; 1,300] per summer. As this group of prey is mainly eaten by deep-diving cetaceans (beaked and sperm whales), its consumption is widespread throughout the Mediterranean, yet with a slight longitudinal pattern (Fig. 3C and *SI Appendix*). Higher consumption in the western Mediterranean is also observed for krill

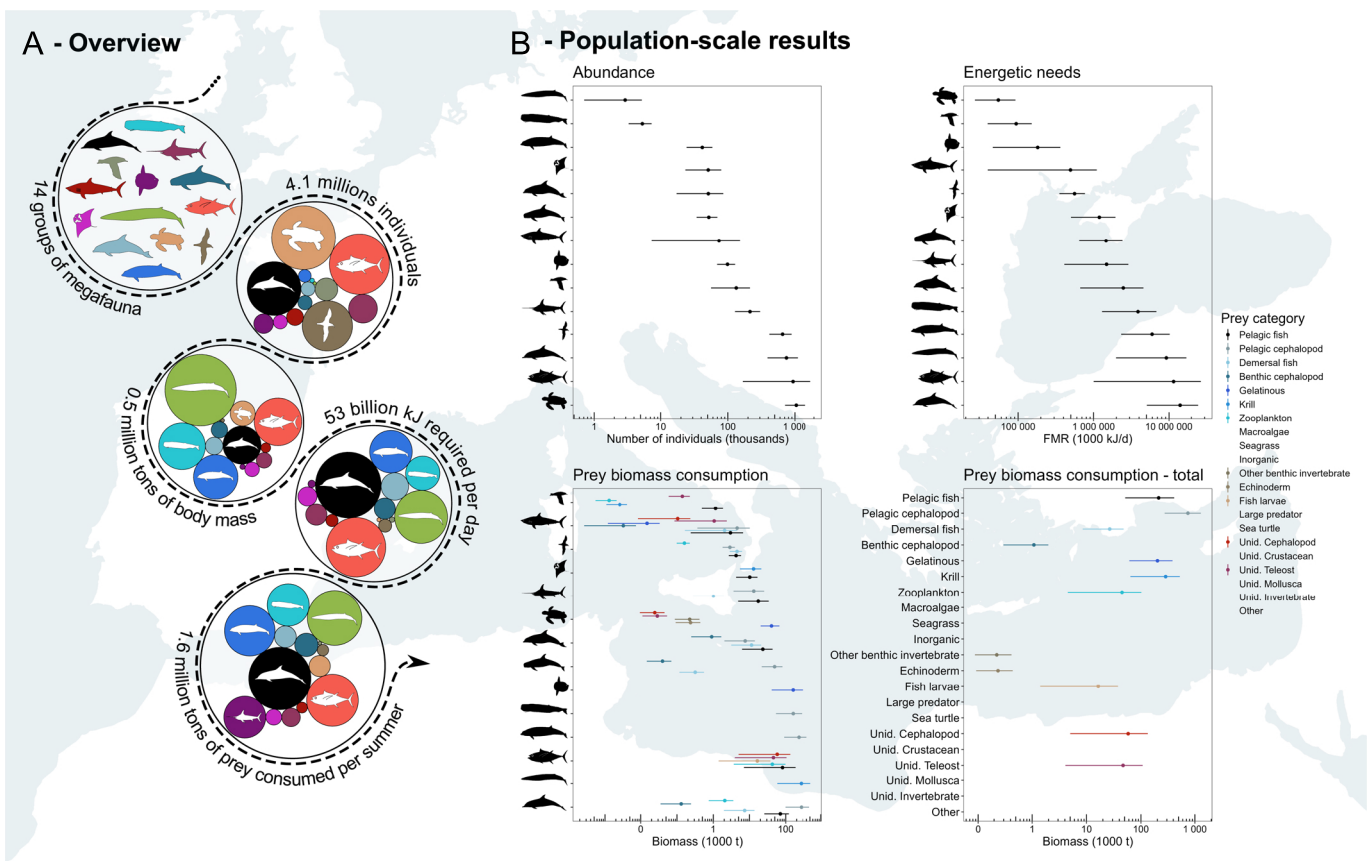
(300 thousand tons [60; 500], mostly extracted by fin whales, spine-tailed devil rays and yelkouan shearwaters), other zooplankton (50 thousand tons [5; 100]), gelatinous prey (200 thousand tons [60; 400], by sunfish and loggerhead turtles), unidentified fish (50 thousand tons [4; 100]), unidentified cephalopods (60 thousand tons [5; 100]) and fish larvae (20 thousand tons [1; 40]). Benthic cephalopods (1,000 tons [300, 200]) and demersal fish (30 thousand tons [10; 50]) are eaten mostly on the continental shelf and slopes of the western and central Mediterranean, while other benthic invertebrates and echinoderms are eaten by loggerhead turtles on the shelves of the central Mediterranean.

## Discussion

Using an energyscape approach, we mapped the food requirements of key species of Mediterranean megafauna during the summer. This community is extremely diverse in terms of species-specific body mass, energetic needs, diet, trophic status, and abundance, with variations in body mass having the largest influence on our estimation of overall biomass consumption (see sensitivity analysis in *SI Appendix*). This community-level energyscape is largely dominated by cetaceans and tunas, which combine high abundance, high life costs, and large body masses. Pelagic cephalopods are the main prey targeted by the community (740,000 tons), followed by pelagic fish (mostly small pelagic fish; 210,000 tons), targeted by cetaceans, tunas, swordfish, sharks, and seabirds (confirming 28). At the other end of the trophic spectrum, a large quantity of zooplankton is consumed (330,000 tons), most of it being krill eaten by fin whales and spine-tailed devil rays. Sunfish and loggerhead turtles, two of the species with the lowest life costs, play a fundamental role in regulating the biomass of gelatinous organisms, with 200,000 tons extracted by these species mostly in the northwestern Mediterranean, confirming a sunfish hotspot in this area (29). Given that jellies and salps are notoriously difficult to detect and quantify in stomach content analyses (30), our estimation of gelatinous plankton biomass consumption may be underestimated, especially for tunas and swordfish (31).

The amounts of energy and biomass processed by the megafauna community confirm its crucial role in nutrient recycling. Indeed, the biomass they consumed is not a removal, but rather a conversion, whereby essential nutrients are remobilized, to the benefit of lower trophic levels (1, 7). In the northwestern Mediterranean, most nutrients are probably recycled by cetaceans and tunas; Scopoli's shearwaters and loggerhead turtles ensure most of the turn-over in the central Mediterranean (benthic prey for turtles, pelagic prey for shearwaters), while deep-diving cetaceans support the productivity of offshore areas by ensuring the vertical remixing of nutrients there.

Spatially, the western Mediterranean strongly stands out as a major megafauna hotspot, both in terms of abundance and energetic needs, resulting in the highest levels of consumed prey biomass. This subregion of the Mediterranean has previously been identified as the most diversified (15) but is also the most anthropized and the most polluted (32–35). Furthermore, the northwestern basin is also where most fisheries operate in the Mediterranean (36). This spatial co-occurrence of megafauna and fisheries may effectively result in direct competition and increase bycatch risk (37, 38). For some species however (e.g. shearwaters), this co-occurrence may be beneficial, as individuals have learned to forage on the fishery discards, yet with deleterious consequences when interactions result in bycatch (39, 40).



**Fig. 4.** (A) Relative contribution of considered megafauna groups to the total megafauna abundance, biomass, energy requirement, and consumed prey biomass in the Mediterranean. The area of each circle is proportional to the contribution of the species to the sums. Circles are color-coded according to the megafauna species they represent. (B) Abundance, energy requirements, and prey biomass consumed by each megafauna species, as well as the total biomass of prey functional groups consumed by the whole megafauna community. The contribution of the Scopoli's shearwater to abundance, biomass, and energy requirements does not include that of their chicks (but their contribution to consumed prey biomass does). In (B), panels are sorted from largest to smallest group-scale values except for prey biomass consumption where species are sorted from the largest to smallest total prey consumption, pooling all prey groups.

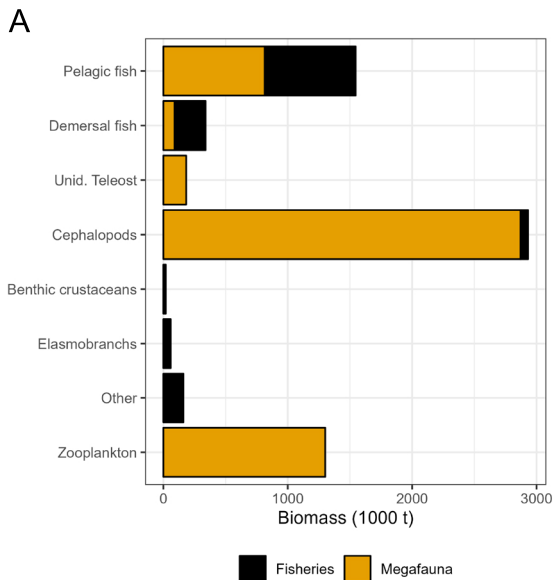
Our biomass estimations concern the summer period, spanning from late June to late August (92 d). We cannot reliably extrapolate these values to the whole year because i) megafauna spatial abundance distributions vary seasonally for many species (some even migrating out of the Mediterranean, such as tunas and shearwaters), and because ii) energetic needs change in winter, especially for species whose reproduction costs occur in summer. The energetic needs of loggerhead turtles and fish, whose metabolism is temperature-dependent, may also change in winter (41), but this may be negligible (see sensitivity analysis in *SI Appendix*). Given these changes in needs and overall abundance, we may presume that the biomass consumed by the Mediterranean marine megafauna during winter is smaller than during the summer season.

As a thought experiment, if we assume that megafauna biomass extraction remains at summer levels year-round in order to compare the biomass extracted by fisheries (which are only available at the year scale), we find that, in the Mediterranean, the overall biomass consumed by megafauna exceeds that extracted by fisheries (Fig. 5), which is coherent with other studies [Pacific Ocean, (20); Atlantic Ocean, (24); Mediterranean Sea, (37, 38); globally, (22)]. We also offer evidence that competition between Mediterranean megafauna and fisheries only concerns a few taxa, mostly fish (Fig. 5): Fisheries extract about one million tons of fish per year, just as much as the estimated consumption by marine megafauna. Within these two million

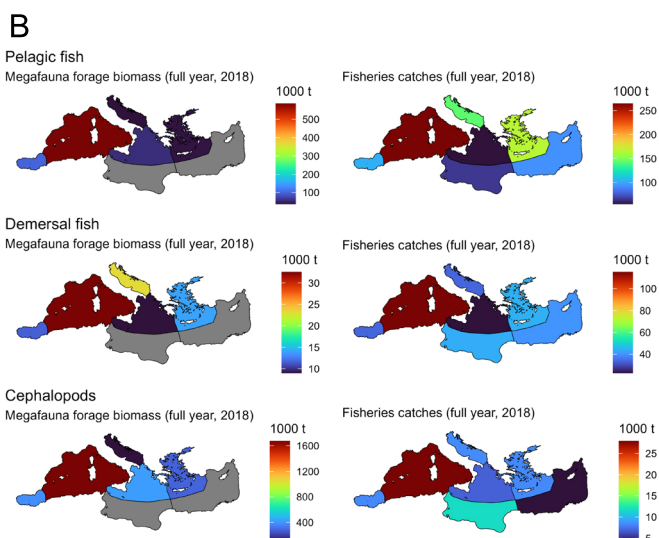
tons, competition probably occurs for only a small proportion of species of commercial interest, in particular small- and medium-sized pelagic fish (20, 24, 37, 38), and mostly within the continental shelves and slopes where most fisheries operate (42). By comparison, competition is probably low for cephalopods, with only a handful of species marginally exploited by fisheries whereas the megafauna consumes a large amount and a large variety of species (60,000 tons caught versus 2,900,000 tons consumed by megafauna, when extrapolating to the whole year). This low level of competition is probably also mediated by a limited spatial overlap, since most cephalopods consumed by megafauna are eaten in the deep sea rather than on the shelves or slopes.

Overfishing thus remains a major issue to be addressed on the shelves of the western Mediterranean to preserve both the exploited fish and megafauna populations. Intense fishing activities provoke resource shortages and increased competition (23), but also induce a shift in the size distribution of fish populations, with the largest size classes being systematically exploited by fisheries (43, 44). Such changes may affect predator's diet composition, energy acquisition, and foraging strategies (45), thereby directly impacting ecosystem structure and functioning (43).

Our results highlight the need for efficient and ambitious protection schemes for the conservation of marine megafauna but also for adequate resource management of lower trophic



Not considering Levantine Sea and Tunisian plateau/gulf of Sidra ecoregions in fisheries data, and extrapolating megafauna biomass consumption to the whole year



**Fig. 5.** Comparison of the biomass extracted by the megafauna community extrapolated for the whole year (which is an overestimation; see text for details) and that extracted by fisheries in each marine ecoregion of the Mediterranean (data only available at the year scale). The fisheries data are extracted for the year 2018 from the Sea Around Us project, so that the catches data match the year for which predator abundances were estimated. In (A), fisheries data exclude the Levantine Sea and Tunisian plateau, and the megafauna biomass consumption maps have been cropped to the extent of fisheries data for comparability between the two datasets. In (B), the spatial distribution of the megafauna biomass consumption and fisheries catches are shown per marine ecoregion. Grey color indicates no value is available for the given area.

levels on which they rely. By focusing on energy content and functional traits rather than on species, energyscapes emphasize the need to preserve energy fluxes across food webs. This approach is complementary of biodiversity-based conservation schemes, as it clarifies and rates, in energetic terms, the disproportionate importance of marine megafauna as trophic keystone species (1, 46). In the Mediterranean, our results for example demonstrate the importance of preserving healthy and abundant populations of species like cetaceans and tunas. The loss of such ecosystem engineers in this region would likely trigger cascading effects with deep changes in the trophic structure of the whole regional

large marine ecosystems (47). This has probably been the case in the past following tuna overfishing (48), the decline of common dolphins (49), and the eradication of the Gulf of Cadiz fin whale population (50).

The energy-centered point of view we develop here aligns with the rationale of ecosystem-based and ecocentric approaches (51), all pointing toward a functional approach of fisheries management and conservation strategies which would preserve functions rather than taxa. Effectively incorporating such changes of perspective in the management plans of Marine Protected Areas (e.g. Pelagos Sanctuary) is key to making them more than “paper parks” (52, 53), and would, ultimately, help in preserving and maintaining ecosystem functioning and the services all marine giants provide to us, humans.

## Materials and Methods

All analyses were done in R version 4.2.3 (54) with a dedicated R package built for this work: energyscapes version 0.1.0 (55).

**The Mediterranean Megafauna Community.** In this study, we focused on the pelagic functional megafauna species, which are repeatedly present at the sea surface and/or mostly or regularly use the upper water column (epipelagic layer). In the Mediterranean, 58 species match this definition, organized into 11 different taxonomic groups (Fig. 1), of which 41% (24 species, Table 1) were included in the present study. Abundance distribution data were insufficient for Myliobatidae and Coryphaenidae to be included in the analysis. For the other species, the availability of distribution data (see below) conditioned the taxonomic level considered for the analyses (species, family, taxa): Xiphiidae, Mobulidae, and Molidae had distribution data available at the species level; for reptiles, only information on loggerhead turtle (*Caretta caretta*) was available; distribution information was available for four out of six species of tunas, but not at the species levels so tunas were considered as a stand-alone group; similarly, sharks were considered as a single group since no species-specific information was available; cetaceans were considered at the species level; distribution information was only available for two seabird species (10%). Some additional details about the species not included in the analysis are provided (see Representativeness of the Results).

**Megafauna Abundance Maps.** We used the best available abundance maps produced during previous studies in the Mediterranean Sea. During the summer of 2018 (June–August), an aerial survey effort was conducted (the ACCOBAMS Survey Initiative, ASI), which spanned 77% of the Mediterranean basin. Most of our abundance maps were derived from this effort, completely or partially. Abundance maps of striped, bottlenose and Risso’s dolphins, fin whales, sharks, spine-tailed devil rays, swordfish, sunfish, tunas, and yelkouan shearwaters were constructed with Density Surface Models entirely based on ASI data (56). Scopoli’s shearwaters are subject to particular detection bias as the birds show some variations in their activity budget along the day, necessitating to tailor a species distribution model (SDM) to correct for this specific bias (first modeling the presence from ASI data, then converting to abundance using the most recent colony censuses; 59). Abundance maps of sperm whales, beaked whales, and loggerhead turtles were built with SDM based on the compilation of several dedicated observation surveys conducted in the Mediterranean in recent years (aerial and boat-based surveys; 57, 58).

All maps came in different projections and resolutions depending on their sources: Maps from ref. 56 were in NAD27 projection at a 0.2° resolution; maps from ref. 57 were in World Geodetic System 1984 (WGS 1984) at a 0.083° resolution; maps from ref. 58 were in a custom Lambert azimuthal equal-area projection, at a 5 km resolution; Scopoli’s shearwater map was in WGS 1984 at 0.042° resolution (59). All maps were reprojected on a regular 0.2° resolution grid in WGS 1984 projection, using a bilinear interpolation for sperm whale, beaked whale, loggerhead turtle, and Scopoli’s shearwater maps.

When deriving abundance estimates of marine underwater organisms from visual surveys, it is crucial to take into account the availability bias. This bias arises where individuals do not spend their entire time at the sea-surface, i.e. they can be present but not available to detection by observers. This is particularly acute for air-breathing deep-diving species, such as beaked or sperm whales, but also for fish species that may have no requirements to surface. To correct for availability bias, we assessed the amount of time each species spends within the first ten meters of the water column, which is the maximum depth at which observers are able to spot cruising animals during aerial surveys (when conditions are perfect). This correction thus permits us to derive the abundance of the species across the whole water column, effectively integrating the vertical dimension in an otherwise 2D analysis (Table 1).

Here, abundance maps for beaked and sperm whales and for loggerhead turtles were already corrected for availability (0.09 for beaked whales, 0.2 for sperm whales, 0.27 to 0.48 for loggerhead turtles), so no further correction was applied. For the other species groups, correction factors were obtained by averaging values gathered in published literature, considering the percentage of time spent between the surface and 10 m deep derived from tags recording diving profiles when possible, or the estimated availability at the sea surface (for striped and bottlenose dolphins).

Seabirds are the only central-place foraging species considered in the present work. They are colonial and synchronized breeders, which means all reproductive individuals raise their chicks at the same period of the year in a few well-defined locations (islands and coast). In June-August, the yelkouan shearwaters are

nonbreeding, but the Scopoli's shearwaters are in the chick-rearing phase, meaning breeding adults perform foraging trips aimed at both their own subsistence and provisioning their chicks. As a consequence, the breeding fraction of seabird populations remove prey biomass corresponding to their own energetic needs, but also to that of their chicks. To include this aspect into our study, we built a map of the abundance of "equivalent chicks," by converting the total abundance map into the abundance of adult breeders (48.5% of the population; see 59) and by halving it by two (this species raises one chick per pair).

**Energy Requirements.** We took advantage of the allometric scaling of individual metabolic rates with body mass to estimate group-specific field metabolic rates (*FMR*, in *kJ/d*). Allometric equations estimate *FMR* from body mass (*M*) as a function of the form  $FMR = \gamma \times M^\theta \times \eta T$ , where  $\gamma$  and  $\theta$  are group-specific scaling parameters and  $\eta$  is the effect of temperature (*T*) for ectotherms. Here, we used the scaling equations built at the lowest taxonomic level from the literature (Table 2), following refs. 27 and 88 for cetaceans, ref. 87 for turtles, ref. 41 for fishes, and ref. 89 for birds.

In the case of cetaceans and turtles, *FMR* was estimated by estimating the Basal Metabolic Rate (*BMR*) from *M*, then by multiplying it by the cost of living (or active metabolism factor,  $\beta$ ; higher values mean more expensive life style). For cetaceans, we used  $\beta$  values from ref. 88 ( $\beta = 3$  for striped dolphins, bottlenose dolphin, and fin whale;  $\beta = 2$  for Risso's dolphin, Cuvier's beaked whale and sperm whale). For turtles, we used the lower range of vertebrate values (2.5).

**Table 1. Megafauna taxonomic groups considered in the study, detailing species composition, correction factors applied to correct for availability bias (\* indicates the availability was corrected in the original abundance map) and source of abundance map**

Group	Composition	Family	Correction factor	Source of abundance map
Striped dolphin	Striped dolphin <sup>†</sup> ( <i>Stenella coeruleoalba</i> )	Delphinidae	0.61 (60)	a
Bottlenose dolphin	Bottlenose dolphin <sup>†</sup> ( <i>Tursiops truncatus</i> )	Delphinidae	0.70 (61–63)	a
Risso's dolphin	Risso's dolphin <sup>†</sup> ( <i>Grampus griseus</i> )	Delphinidae	0.48 (64)	a
Sperm whale	Sperm whale <sup>†</sup> ( <i>Physeter macrocephalus</i> )	Physeteridae	0.20*	b
Cuvier's beaked whale	Cuvier's beaked whale <sup>†</sup> ( <i>Ziphius cavirostris</i> )	Ziphiidae	0.09*	b
Fin whale	Fin whale <sup>†</sup> ( <i>Balaenoptera physalus</i> )	Balaenopteridae	0.55 (65)	a
Loggerhead turtle	Loggerhead turtle <sup>†</sup> ( <i>Caretta caretta</i> )	Cheloniidae	0.27–0.48*	c
Sharks	White shark <sup>†</sup> ( <i>Carcharodon carcharias</i> ), Short-fin mako <sup>¶</sup> ( <i>Isurus oxyrinchus</i> ), Porbeagle <sup>‡</sup> ( <i>Lamna nasus</i> )	Lamnidae	0.43 (66–73)	a
	Spotted ragged-tooth shark <sup>‡</sup> ( <i>Carcharias taurus</i> )	Odontaspidae		
	Scalloped hammerhead shark <sup>§</sup> ( <i>Sphyrna mokarran</i> ), Smooth hammerhead shark <sup>¶</sup> ( <i>Sphyrna zygaena</i> )	Sphyrnidae		
	Blue shark <sup>†</sup> ( <i>Prionace glauca</i> ), Spinner shark <sup>§</sup> ( <i>Carcharhinus brevipinna</i> )	Carcharhinidae		
	Thresher shark <sup>†</sup> ( <i>Alopias vulpinus</i> )	Alopiidae		
Spine-tailed devil ray	Spine-tailed devil ray <sup>†</sup> ( <i>Mobula mobular</i> )	Mobulidae	0.49 (74)	a
Swordfish	Swordfish <sup>†</sup> ( <i>Xiphias gladius</i> )	Xiphiidae	0.13 (75, 76)	a
Tunas	Albacore tuna <sup>†</sup> ( <i>Thunnus alalunga</i> ), Atlantic bluefin tuna <sup>‡</sup> ( <i>Thunnus thynnus</i> ), Skipjack tuna <sup>†</sup> ( <i>Katsuwonus pelamis</i> )	Scombridae	0.32 (77–80)	a
Sunfish	Ocean sunfish <sup>†</sup> ( <i>Mola mola</i> )	Molidae	0.30 (81–86)	a
Scopoli's shearwater	Scopoli's shearwater <sup>‡</sup> ( <i>Calonectris diomedea</i> )	Procellariidae	-	d
Yelkouan shearwater	Yelkouan shearwater <sup>†</sup> ( <i>Puffinus yelkouan</i> )	Procellariidae	-	a

References used to determine the correction factors are indicated in parentheses alongside the values. Abundance maps are from a: (56); b: (57); c: (58); and d: (59).

<sup>†</sup>The species is present year-round in the Mediterranean Sea (but regional movements can occur seasonally).

<sup>‡</sup>The species is migratory, i.e. leaves the sea during part of the year.

<sup>§</sup>The species is occasional in the Mediterranean.

<sup>¶</sup>The large-scale movements of the species have not yet been determined for the Mediterranean.



**Table 2. Allometric equations relating body mass  $M$  (in g) to  $FMR$  for each species group**

Species	FMR formula	Original unit	Correction factor
Cetaceans	$\beta \times (293.1 \times M^{0.75})$	kJ/d	–
Turtles	$\beta \times (0.67 \times M^{0.65})$	mL <sub>O2</sub> /h	×0.48
Fishes	$0.56 \times M^{0.94} \times \exp(0.02 \times Temp)$	mg <sub>O2</sub> /h	×0.36
Shearwaters	$23.33 \times M^{0.56}$	kJ/d	–

Where necessary, the  $FMR$  was converted to kJ/d using the specified correction factor.

We built the statistical distribution of  $\beta$  parameters using a truncated normal distribution with a 20% SD (truncating between 1 and 5).

It must be noted here that the allometric equation of  $FMR$  for shearwaters was built using values measured from adults during the reproductive period (89), and thus incorporates the reproduction-driven increase in  $FMR$ . Consequently, energy expenditure was most probably slightly overestimated for about half of the Scopoli's shearwaters (where 51.5% of the population is composed of nonbreeding individuals, that is encompassing failed adult breeders, immatures, and juveniles), and for the whole population of yelkouan shearwaters, which were nonbreeding at the time period the ASI survey was conducted.

**Body Mass.** We reconstructed body mass distribution across species populations from species-specific sources (Table 3 and *SI Appendix*). The French Stranding Network database was used to reconstruct cetacean body mass distribution from the biometrics of individuals stranded along the French Atlantic and Mediterranean coasts between 1990 and 2021 (Table 3; as the body mass was reconstructed from the body length of stranded individuals (potentially unhealthy or old individuals), we may slightly underestimate the true body mass of the whole population). Data from refs. 90 and 91 were used to reconstruct the body mass distribution of ocean sunfish and loggerhead turtle, respectively. Body mass direct measurements on wild individuals during bioglogging fieldwork were used for Scopoli's shearwater, while body mass distributions were constructed from fisheries data for sharks (92–95), swordfish (96, 97) and tunas (98–102). Only individuals of a body length larger than 20 cm were used for building body mass distributions, for all species, since individuals smaller than this threshold are very unlikely to be detected from plane (i.e. the abundance maps only stand for the fraction of the population with a size larger than 20 cm).

For the fin whale, spine-tailed devil ray, and yelkouan shearwater, body mass distributions were constructed using a normal distribution function with mean and SD extracted from the literature for adult individuals (103–105, using a conservative SE of 10%).

**Table 3. Mean and SD of body mass (kg) for the studied species, the distribution functions used in the analysis, and the source of data used to build the distribution functions**

Species group	Body mass (Mean ± SD)	Distribution	Source
Striped dolphin	62 ± 31	<i>skewed</i> $\mathcal{N}(\mu = 95, \omega = 50, \alpha = -2.5)$	a
Bottlenose dolphin	192 ± 96	<i>skewed</i> $\mathcal{N}(\mu = 300, \omega = 150, \alpha = -1.9)$	a
Risso's dolphin	164 ± 88	$\mathcal{N}(\mu = 164, \sigma = 88)$	a
Cuvier's beaked whale	1,513 ± 660	<i>skewed</i> $\mathcal{N}(\mu = 2, 100, \omega = 1, 000, \alpha = -1.5)$	a
Sperm whale	13,068 ± 8,133	$\mathcal{N}(\mu = 13, 068, \sigma = 8, 133)$	a
Fin whale	55,000 ± 11,000*	$\mathcal{N}(\mu = 16, 851, \sigma = 10, 884)$	b
Loggerhead turtle	18.9 ± 14.3	<i>Weibull</i> ( $\lambda = 1.39, k = 21.14$ )	c
Sharks	41 ± 34	<i>skewed</i> $\mathcal{N}(\mu = 15, \omega = 26, \alpha = 6)$	d
Swordfish	36 ± 26	<i>Gamma</i> ( $\kappa = 2.61, \theta = 0.07$ )	d
Tunas	77 ± 74	<i>Gamma</i> ( $\kappa = 2.10, \theta = 0.03$ )	d
Spine-tailed devil ray	132 ± 26*	$\mathcal{N}(\mu = 132, \omega = 10)$	e
Ocean sunfish	9 ± 8	<i>Gamma</i> ( $\kappa = 2.04, \theta = 0.23$ )	f
Scopoli's shearwater	0.61 ± 0.06	$\mathcal{N}(\mu = 0.611, \sigma = 0.06)$	g
Yelkouan shearwater	0.44 ± 0.04	$\mathcal{N}(\mu = 0.435, \omega = 0.035)$	h

The construction of body mass distribution functions is detailed in *SI Appendix*. \*unknown variability around the mean, so apply a conservative sd (20% of the mean). <sup>a</sup>body mass reconstructed from French Stranding Network data; <sup>b</sup>mean mass and associated SD from ref. 103; <sup>c</sup>body mass distribution built from data from ref. 91; <sup>d</sup>body mass reconstructed from fisheries data; <sup>e</sup>mean body mass derived from mean body length in FishBase (105); <sup>f</sup>body mass distribution built from data from ref. 90; <sup>g</sup>body mass distribution built from wild animal measurements; and <sup>h</sup>mean mass and associated SD from ref. 104.

**Sea Surface Temperature.** Metabolic rates are directly dependent upon water temperature for fishes. We computed the seasonal mean and SD of the sea surface temperature across the Mediterranean Sea to provide the range of possible temperature conditions experienced by fish species during the study period in each map cell. This seasonal summary was computed from daily sea surface temperatures from June, first 2018 to August, 31st 2018 (the time period of the ASI survey), accessed from the E.U. Copernicus Marine Service (<https://marine.copernicus.eu/>, product "MED-SEA\_MULTIYEAR\_PHY\_006\_004," [https://doi.org/10.25423/CMCC/MEDSEA\\_MULTIYEAR\\_PHY\\_006\\_004\\_E3R1](https://doi.org/10.25423/CMCC/MEDSEA_MULTIYEAR_PHY_006_004_E3R1)). We neglected the variation in temperature across the water column, since the abundance maps are based on individuals present within the first ten meters below the surface.

**Diet Taxonomic and Energetic Composition.** Building energyscapes necessitate information on the diet composition, expressed in wet weight (derived from stomach contents). We retrieved such information for cetaceans from refs. 37 and 42, for tunas from fisheries data (reviewed in refs. 106 and 107), for loggerhead turtle from refs. 108 and 109, for swordfish from refs. 110 and 111, for yelkouan shearwater from ref. 112, for Scopoli's shearwater from ref. 113 (assuming the diet of Scopoli's shearwater is highly similar to its close counterpart Cory's shearwater (*Calonectris borealis*; 114), and that the diet of chicks is similar to that of adults), for spine-tailed devil ray from ref. 115. The diet of sharks was constructed from a literature compilation (116–121): The percentages of wet weight per prey species from each study were averaged, and the result standardized to range between 0 and 1.

Converting  $FMR$  to foraged biomass necessitates converting the weight of prey into energy. For that purpose, energetic contents (in  $\text{kJ.g}^{-1}$ ) of individual forage species were retrieved from the literature at the lowest taxonomic level possible (37, 122–125). In absence of species-specific values, we used that of the lowest taxonomic level available. No energetic content (expressed in wet weight) was available in the literature for some taxa (turtles, cetaceans, tunas, seagrass and algae), so the total biomass foraged for these taxa by megafauna was not estimated.

**Foraged Biomass Estimation.** We used a pseudo-Monte-Carlo approach to propagate uncertainty around the parameters (abundance, temperature, body mass) throughout the analysis. Our biomass estimations thus take into account the species-specific ranges of possible abundance, temperature, and body mass values. Foraged biomass was estimated 50,000 times for each species and each prey functional group (using the `mc_simulation` and `bio_cons_est` functions in the `energyscapes` package). For each estimation, we draw the abundance map from a normal distribution with mean predicted abundance and its SD as parameters (a draw was done for each cell with the values of that cell). Similarly, we sampled a body mass value within the body mass distribution of the species. In the case of ectotherms, a temperature map was sampled by drawing from a normal distribution using seasonal mean temperature and its SD as parameters.

Species-specific *FMR* was estimated from the species-specific allometric equations, sampled body mass, and sampled temperature map. The daily ration for a prey item ( $R_j$ , in kg) necessary to maintain an individual predator was estimated by converting the individual energetic requirement (*FMR*) to wet mass of foraged food based on energy content of the given prey item and taking into account the assimilation efficiency ( $\alpha$ ):

$$R_j = \sum \left( \frac{FMR}{\alpha \times IE} \times \%W_j \right),$$

where  $\%W_j$  is the proportion of the food item  $j$  in the diet and *IE* is the ingested energy of the total diet, computed as  $\sum (W_j \times E_j)$  (with  $E_j$  the energy density of prey  $j$ ).  $\alpha$  was set to 0.8 for all species. The total daily ration for a prey functional group is then computed as the  $R = \sum R_j$ .

The forage biomass  $B$  was estimated as  $B = R \times A \times N_{\text{days}}$ , where  $A$  is the abundance map and  $N_{\text{days}}$  is the study period length (92 d; June, July, August). The total energy requirement of a population (the energyscape, expressed as the map of energetic needs of the total population during a single day) was calculated as  $FMR \times A$ .

We stored all estimated quantities for each estimation (energyscape;  $R$  expressed as percentage of body mass;  $B$ ), and computed the mean and 90% CI from their posterior distributions. Resulting maps of foraged biomass were summarized to provide basin-scale estimates of forage species consumption for each predator group (mean and 90% CI).

The total energy requirement of each megafauna species was summarized over the basin, as well as the total consumed biomass of each functional group of prey (pelagic fish, pelagic cephalopod, demersal fish, benthic cephalopod, gelatinous, krill, zooplankton, fish larvae, etc). We also summarized the total biomass consumed by the whole megafauna community by summing the consumptions over the entire basin for each group of prey.

**Seafloor Accessibility Constraint.** Some of the studied species forage both along the water column (pelagic prey) and at the seafloor (benthic and demersal prey). Yet, these species geographically range in areas where benthic and demersal prey are beyond reach, as the seafloor is deeper than the maximum diving depth known for the species. This is the case of loggerhead turtles and striped, bottlenose and Risso's dolphins. In such a configuration, simply estimating the forage biomass from the abundance distribution as described above leads to biased estimates since benthic and demersal prey would be estimated as consumed in areas where the predators are unable to do so (over abyssal plains, for example). To overcome this and effectively consider the vertical distribution of the species, we split the analysis between areas where the species can reach the seafloor and areas where they cannot. This split is species-dependent, as the diving depth varies across species: 200 m for loggerhead turtles (126); 700 m for striped dolphins (127); 300 m for bottlenose dolphins (128); 700 m for Risso's dolphins (129). For loggerhead turtles, we considered the species forages exclusively on gelatinous prey when in areas where the seafloor is beyond reach. For dolphins, we considered the species to exclusively forage on pelagic prey groups in similar proportions as they do elsewhere. Once we ran the analyses for each area separately, we combined the results and summarized daily rations and biomass consumptions as for other groups. Sharks also forage on demersal and benthic prey, but the group being multispecific, with species able to forage on the seafloor even at large depths, we considered benthic and demersal prey to be accessible everywhere. Finally,

Scopoli's shearwater's diet also includes demersal fish species. These species are however not directly accessed by the individuals but rather made available at the surface through fisheries discards (39, 130) so that the accessibility constraint does not apply to the species.

**The Particular Case of Scopoli's Shearwater Chicks.** Scopoli's shearwaters are the only bird species breeding during our study period, so that we need to estimate the biomass of prey extracted by adult shearwaters to feed their chicks. Scopoli's shearwater chicks are not fed every day, and both parents participate to their feeding. Precise information on chick diet and feeding phenology does not exist for Scopoli's shearwater, so we used information from the closely related species Cory's shearwater. The hatching occurs in late July, with a fledging in late October, which represents a feeding period of about 40 d during our study period (June–August). Over that period, chicks are fed rations of 53 to 79 g during 74 to 97% of nights (131). We considered the ration and the proportion of day with meal to be distributed following truncated normal distributions, using values reconstructed from ref. 131 (mean of 66 g and SD of 20%, truncated between 53 and 79 g for ration; mean of 85.5% of days with meal, SD of 10%, truncated between 74 and 97% of days).

Considering the parents fed their chicks with a similar diet to their owns, we estimated the ration for each prey item  $j$  to be  $R_j = R \times \%W_j$ , where  $\%W_j$  is the proportion of item  $j$  in the diet. The total biomass extracted to feed the chicks for each prey item was thus  $B_j = R_j \times A \times N_{\text{days}}$ , where  $N_{\text{days}}$  is the proportion of day with meal and  $A$  the abundance of chicks (half the abundance of breeders).

**Representativeness of the Results.** For cetaceans, the six species we considered represent the vast majority of the cetacean individuals present in the Mediterranean. The five species we were not able to consider in the present work are either occasional visitors (rough-toothed dolphin, *Steno bredanensis*), are only present in the Black Sea (harbor porpoise, *Phocoena phocoena*; 91,000 individuals; 132), or have resident populations occurring in small areas, such as the killer whale (*Orcinus orca*) in the Strait of Gibraltar (ca 40 individuals; 133) or the common dolphin (*Delphinus delphis*; although widespread before the 60s, the species has declined very rapidly and has today shrunk to relict groups in the Alboran, southeastern Tyrrhenian and eastern Ionian Seas as well as around Maltese islands, the Alboran Sea being the only Mediterranean region where the species is still abundant; 49). Our analysis thus accounts for the vast majority of the biomass consumed by cetaceans in the Mediterranean, but it must be noted that the abundance map for bottlenose dolphins probably underestimates the actual abundance of the species in coastal waters.

Although 20 different seabird species can be seen in the Mediterranean, only a handful are truly pelagic (i.e., distributing and foraging in the ocean) and thus of interest to our study. These are the Scopoli's, Cory's, yelkouan, and Balearic shearwaters (*P. mauretanicus*), European storm petrels (*Hydrobates pelagicus*) and terns (Sandwich (*Thalasseus sandvicensis*), common (*Sterna hirundo*), lesser crested (*T. bengalensis*), and little (*Sternula albifrons*) terns). Cory's shearwater population is negligible in the Mediterranean Sea, with only a few pairs breeding in the Chafarinas Islands. Balearic shearwaters are winter breeders and migrate out of the Mediterranean Sea during the summer. These two species were thus considered absent from the study area during our study period. Storm petrel and tern populations in the Mediterranean are small (3,300 individuals for storm petrels, and 14,800 individuals for all tern species from the most recent census; 56). Thus, no abundance maps exist at the Mediterranean scale for these species and we could not include them. Both are mostly present in the western Mediterranean and the Adriatic Sea and consume zooplankton and small pelagic fish.

Finally, the remaining species of seabirds frequenting the Mediterranean in summer are cormorants (exclusively coastal; European (*Phalacrocorax aristotelis*), Great (*P. carbo*) and Pygmy (*P. pygmaeus*) cormorants) and larid species (Mediterranean (*Larus melanocephalus*), black-headed (*L. ridibundus*), little (*Hydrocoloeus minutus*), Audouin's (*L. audouinii*), yellow-legged (*L. michahellis*) and lesser black-backed (*L. fuscus*) gulls). Some species of the latter group can distribute and forage offshore on the continental shelves, but most of the populations remain coastal and forage on terrestrial and tidal resources. We were thus not able to include these species in the analysis due to insufficient information on the abundance and the diet composition of the portions of the populations foraging offshore.

In a nutshell, although we can hypothesize that the two species of seabirds included in the present study are responsible for a large portion of the biomass consumed by seabirds in the Mediterranean, the consumption estimated in the present work is certainly an underestimate of the actual consumption of the whole avian community across the basin, but by how much remains an open question.

Concerning the reptiles, abundance distribution maps were only available for adult loggerhead turtles. This species is by far the most common (nesting throughout the sea), yet we only considered in the present work the consumption of the largest individuals in the population (>20 cm in length), and overlooked the consumption of smaller individuals, which may represent a substantial portion of the total population. These small turtles are mostly oceanic, and overlooking them probably results in an underestimation of the total amount of gelatinous prey consumed by loggerhead turtles in the Mediterranean. Still, four other species can be seen in the Mediterranean: the green turtle (*Chelonia mydas*), which also breeds in the Mediterranean (mostly in the eastern basin) as well as the hawksbill (*Eretmochelys imbricata*), Kemp's ridley (*Lepidochelys kempii*), and leatherback (*Dermochelys coriacea*) turtles, which are only occasional in the region. The green turtle population has been estimated to range from 263,000 to 1,251,000 individuals, and while adults and larger subadults feed exclusively on seagrass, smaller juvenile turtles have a more omnivorous diet and may be consuming some of the prey species under discussion here (134). However, since no distribution predictions are available for green turtles, they could not be assessed here.

A similar rationale as for loggerhead turtles stands for sunfish, whose population is strongly biased toward smaller-sized individuals (90). This means we miss a large part of the population (individuals smaller than 20 cm), and thus probably underestimate the consumption of gelatinous prey. However, stable-isotope analyses have hinted that sunfish are more benthic foragers than previously thought (135), especially small-sized individuals. Our assumption of a fully gelatinous diet therefore probably also results in an underestimation of benthic prey consumption by the species on the shelves.

Abundance information is deficient for Coryphaenidae (Common dolphinfish, *Coryphaena hippurus*) and Myliobatidae (eagle ray, *Myliobatis aquila*), and we cannot infer by how much we underestimate the total biomass consumed by the megafauna community when not incorporating them.

The basking shark (*Cetorhinus maximus*) was the only pelagic shark species not included in our study. This species can easily be seen from a plane and is one of the few shark species which can be identified with certainty during aerial surveys. Yet, only a few individuals were sighted during the ASI, which precluded any abundance estimation for this species from these data. As a consequence, the species was not included, which most probably led to underestimating the zooplankton consumption by the megafauna community.

The "tunas" category from the ASI data included albacore, Atlantic bluefin, and skipjack tunas. These species are the three largest Scombridae species present in the Mediterranean and are the ones most likely sighted during the ASI surveys. Two related species are however present in the Mediterranean which also match our pelagic megafauna criteria, the little tunny (*Euthynnus alletteratus*) and the Atlantic bonito (*Sarda sarda*). These two species are of smaller size and are unlikely to be sighted from the aerial survey, so the present study does not include them. Excluding these two species probably results in underestimating the total amount of small pelagic fish consumed by the megafauna community.

The Mediterranean monk seal is the only pinniped species inhabiting the Mediterranean Sea. The species is mostly present in the Greek peninsula, but

the species is today reduced to less than 700 individuals (including the Atlantic remnant subpopulations). Therefore, including the species would not change much the final estimates presented in this study.

**Data, Materials, and Software Availability.** R codes developed to conduct the present study are made available in the following Zenodo repository (136). The analyses presented in the manuscript build up from data and products previously published in various publications: (56–59).

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