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Review Article

Big data approaches to the spatial ecology and conservation of marine megafauna

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Satellite remote-sensing and wildlife tracking allow researchers to record rapidly increasing volumes of information on the spatial ecology of marine megafauna in the context of global change. This field of investigation is thereby entering the realm of big data science: Information technology allows the design of completely new frameworks for acquiring, storing, sharing, analysing, visualizing, and publicizing data. This review aims at framing the importance of big data for the conservation of marine megafauna, through intimate knowledge of the spatial ecology of these threatened, charismatic animals. We first define marine megafauna and big data science, before detailing the technological breakthroughs leading to pioneering "big data" studies. We then describe the workflow from acquiring megafauna tracking data to the identification and the prediction of their critical habitats under global changes, leading to marine spatial planning and political negotiations. Finally, we outline future objectives for big data studies, which should not take the form of a blind technological race forward, but of a coordinated, worldwide approach to megafauna spatial ecology, based on regular gap analyses, with care for ethical and environmental implications. Employing big data science for the efficient conservation of marine megafauna will also require inventing new pathways from research to action.

Introduction

In 1998, Daniel Pauly and his team used fisheries data collected by the Food and Agriculture Organization, to demonstrate the global extent of overfishing (Pauly *et al.*, 1998). Their landmark publication is one of the pioneering examples of analysing big data to address marine conservation issues. More specifically, the paper dealt with the spatial ecology of marine megafauna, as it employed novel analytical tools to show the gradual disappearance of large predatory fish from the world's oceans. Pauly described his rationale as follows: "In the late nineties, people were realizing that fishing is actually a problem for the oceans. To figure out if this activity is in the process of wiping itself out, you have to go beyond the Bay of Whatchamacallit or the Gulf of Whatever. When astrophysicists can't see something well enough, they build a bigger telescope. So that's what I did, build a bigger machine, the biggest one I could imagine—the world since 1950" (Grémillet, 2021).

Ecology is a complex science because of the multitude of biotic and abiotic factors affecting natural processes at vast spatio-temporal scales, and because logistics constraints make it difficult to conduct experiments. Multifactorial analyses therefore call for big data approaches, able to handle increasingly large and heterogeneous datasets. Also, ecologists often suffer from spatial and temporal short-sightedness (Pauly, 1995), and worldwide approaches combined with deeper historical perspectives are urgently needed.

With respect to environmental sciences, there is a correlation between the successive technological revolutions and global changes. Breakthroughs, such as the invention of the internal combustion engine in the 19th century, and of the microchip in the 20th century, gave humanity unprecedented power to exploit natural resources and to modify its environments. Technological advances also provided scientists with powerful tools to study the consequences of unrestrained human development on terrestrial and marine ecosystems. Those notably include electronic technologies, which allowed generating, storing, sharing, and analysing large volumes of data, to address research questions in Ecology.

In the oceans, ecological knowledge often lags behind that achieved for terrestrial biota, notably for observing marine megafauna in its natural environment. This initial handicap forced marine scientists to invent new methods, to fathom the unknown. This is notably the case of remote sensing, which revolutionized oceanography following the launch of Nimbus 7 in 1978. This satellite carried a multispectral radiometer, recording the first large-scale measurement of primary productivity at the ocean surface. Satellites with many other sensors followed, measuring a great variety of biotic and abiotic, static, and dynamic ocean variables (Goddijn-Murphy *et al.*, 2021). Around the same time, microchip technologies allowed the design of satellite transmitters light enough to be carried by large fish, marine mammals, turtles, and seabirds (Timko and Kolz, 1982). This breakthrough revolutionized the spatial ecology of marine megafauna, which could then be tracked anywhere on the planet. Marine megafauna includes 30% threatened species, more than any other group of marine species (Pimiento *et al.*, 2020). Knowledge of their whereabouts across all oceans, and of environmental conditions shaping their movements, is key to the conservation of this suite of marine animals, notably through the designation and implementation of protected areas (Pichegru *et al.*, 2010; Hindell *et al.*, 2020). Many elements of marine megafauna are charismatic, and studying their spatial ecology often yields dramatic results about their ocean voyages and the ecological functioning of marine systems, displayed widely using

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attractive maps and animations. Therefore, studying the spatial ecology of marine megafauna is also a powerful means to gain public support for marine conservation, and to win the interest of decision-makers (Hays *et al.*, 2016).

Over the last two decades, large volumes of data on the spatial ecology and conservation of marine megafauna have been collected. As handling, storing, and manipulating such data are becoming increasingly difficult, researchers are now expanding their activities towards the field of information technology, thereby entering the realm of big data science. Yet, where does this technological race lead us to? In this review, we first define marine megafauna and big data, before detailing the variety of approaches used to study the spatial ecology and conservation of marine megafauna with big data. We then address the technological challenges of collecting and analysing such big data, and of translating research findings into operational conservation measures for threatened marine megafauna. Finally, based on this knowledge, we outline the way forward.

What are marine megafauna and big data?

In a strict sense, megafauna is defined as any adult creature weighing more than 45 kg (Pimiento *et al.*, 2020). In the sea, this includes some bony fish and elasmobranchs, reptiles (sea turtles), a seabird (the Emperor penguin, *Aptenodytes forsteri*), as well as most marine mammals, several species of molluscs and cnidaria. Yet, this definition varies a lot according to biota (marine vs. terrestrial), groups of species (e.g. birds vs. mammals), and scientific communities (palaeontologists vs. ecologists). Overall, a definition of megafauna primarily based on body mass seems reductive. This is because such a threshold does not reflect the potential importance of smaller-sized species, which may also act as ecological engineers and keystone species within trophic webs and at the landscape scale. For this reason, Moleón and colleagues (Moleón *et al.*, 2020) recently proposed the extended definition of functional megafauna. This operational definition is particularly relevant across environmental contexts and taxonomic groups, because it better reflects the trophic significance of single species. For instance, in a provocative manner, one may consider that the little auk (*Alle alle*), one of the smallest seabirds in the North Atlantic, is marine megafauna. Indeed, the little auk is one of the most numerous seabirds in the world (40–80 million individuals), capable of extracting up to 24% of zooplankton stocks in certain areas, and of transforming entire coastal landscapes by carrying tonnes of nutrients from sea to shore with its guano (González-Bergonzoni *et al.*, 2017). Therefore, for this review, we took a functional look at marine megafauna, by also including smaller (but trophically important) species.

Defining "big data" can be equally challenging. There is the general perception that big data is a large volume of information generated from complex and multiple data sources, which cannot be handled, analysed, stored, and shared with common tools. Also, growth in data volume and complexity seems an adequate metric to identify big data. For instance, wildlife tracking depicting the at-sea movements of marine megafauna only consisted of tens of data points when based on radio-tracking in the 1970s. This field of investigations abruptly entered in the "big data" area from the early 2000s, with the advent of GPS recorders, accelerometers, magnetometers, and other bio-logging tools, which were at once yielding millions of data points (Ropert-Coudert and Wilson, 2005; Tournier *et al.*, 2021). More generally, big data is defined along the lines of the four Vs (Yang and Huang, 2013; Farley *et al.*, 2018):

Volume refers to the size of the data,

Velocity indicates that big data are sensitive to time,

Variety means big data comprise various types of data with complicated relationships, and

Veracity indicates the trustworthiness of the data.

Overall, the occurrence of big data reflects the capacity of a specific research community to deal with this flood of bytes: If you at once struggle to handle a large data set, to the point that you have to invent completely new tools to check, store, analyse, and share information, be sure that you are working with big data.

Studying the spatial ecology of marine megafauna with big data

The spatial ecology of marine megafauna can be studied using a great variety of methods (Figure 1). Yet, this research field is based up to 60% (Web of Science, Nov 2021) on electronic tracking data of animal movements (e.g. satellite transmitters, GPS), and on bio-logging [*sensu* (Ropert-Coudert and Wilson, 2005)]. Also, beyond simple positioning information, tracking, and bio-logging have the great advantage of providing fine-scale, three-dimensional information on animal movement. We will therefore mainly detail big data tracking/bio-logging studies of marine megafauna, but will first briefly address some alternative methods.

(1) Historically, information on the whereabouts of marine animals was compiled from direct observations performed on land, and from vessels and aircraft. These sightings concern unidentified individuals (Grémillet *et al.*, 2017), or marked animals, for instance, ringed seabirds of known origin. Occurrence data and ring recoveries were used to sketch the first species-specific, global distribution atlases of marine megafauna (e.g. (Harrison, 2000)). Originally designed to inform naturalists, these atlases are still essential information sources, notably for retrospective analyses of global change impacts on marine megafauna, in a spatial context (Grémillet *et al.*, 2018a). These also integrate population processes, which can be studied via capture–mark–recapture schemes (Omeyer *et al.*, 2019), and they are being expanded rapidly by inputs from citizen sciences, notably through GBIF and OBIS-SEAMAP.

(2) Underwater baited cameras, operated either remotely or by divers, also emerged as powerful tools to study the distribution of marine megafauna. They were initially designed to study rare marine species (Hessler *et al.*, 1972) and scavengers in abysses (Priede *et al.*, 1991). Meanwhile, they are used around the world, notably as a cost-efficient way to study fish assemblages (Langlois *et al.*, 2010), and recorded videos and audios generate big data, which can fuel international networks of researchers. This also applies to hydrophone networks, used for the passive acoustic monitoring of marine megafauna (e.g. (Hauser *et al.*, 2017; Stafford *et al.*, 2018)).

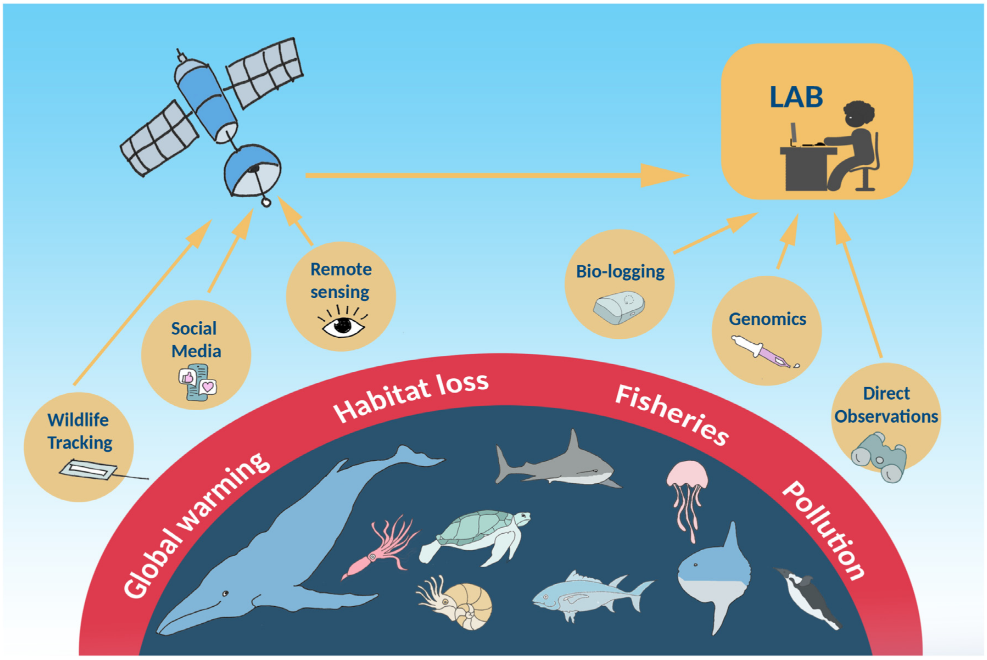

Figure 1. Acquiring big data on the spatial ecology of marine megafauna.

(3) More recently, environmental DNA (eDNA) metabarcoding emerged as a completely new way to identify individuals, species, and communities, to track their movements and distributions, and study biological diversity across time and space (Taberlet *et al.*, 2018). This approach brings streams of big data and its own methodological challenges (Mathon *et al.*, 2021), but is booming in the context of marine conservation (Boulanger *et al.*, 2021). Beyond studying the current occurrence of marine megafauna, genomics studies also allow assessments of past abundances and distributions, and modelling of future dynamics (Cristofari *et al.*, 2018).

(4) With respect to bio-logging studies of marine megafauna, the advent of big data occurred much earlier for certain species and taxa, and according to tag type: Accelerometry, video, and acoustic tags generated data sets, which were substantially larger and more complex than simple positioning devices.

Due to massive economic interests linked to bluefin tuna (*Thunnus thynnus*), this species was probably the first element of marine megafauna subjected to a "big" tracking studies, released in 2005 (Block *et al.*, 2005). These insights gained using satellite tracking of 330 individuals were essential in a conservation context, because they revealed two distinct, yet connected stocks of bluefin tuna in the eastern and western North Atlantic. Around the same time, first big tracking studies of seabirds also occurred (Grémillet *et al.*, 2004), mainly because some of the larger seabirds are easily accessible when they breed on land, and can be fitted with GPS recorders unravelling their at-sea movements. Big tracking studies of other marine megafauna proved far more challenging, but spectacular results also appeared for elephants seals (*Mirounga leonina)* and leatherback sea turtles (*Dermochelys coriacea*) from the mid-2000s (Biuw *et al.*, 2007; Georges *et al.*, 2007; Charrassin *et al.*, 2008). Those demonstrated the astonishing three-dimensional movement capabilities of these large species, and their potential as samplers of oceanographic variables in the deep ocean (Chambault *et al.*, 2017; Treasure *et al.*, 2017).

Once electronic tags became cheaper, they could be fitted at multiple sites, and big single-species tracking studies soon embraced meta-population processes, as in northern gannets (*Morus bassanus*), which displayed inter-colony at-sea space partitioning (Wakefield *et al.*, 2013). From there, the community level was reached by the TOPP program (Tracking of Pacific Predators), which recorded the movements of 23 species of whales, seals, turtles, fish, and seabirds on an ocean-basin scale (Block *et al.*, 2011). Nowadays, there are significant efforts made to perform truly global studies of the spatial ecology of marine megafauna using bio-logging. Seabirds are probably the most studied group in this respect (Strøm *et al.*, 2021), with tracking information available for 212 species out of 363 (Bernard *et al.*, 2021), and the global seabird tracking database curated by BirdLife International containing >17 million data points. First multispecies/global studies concerning shark movements were also recently released (Queiroz *et al.*, 2016, 2019), and similar approaches are underway for sea turtles (Fossette *et al.*, 2014), facilitated by the State of the World's Sea Turtles Project. Finally, it is important to keep in mind that marine and terrestrial ecological processes remain tightly linked. To embrace this additional dimension, the largest tracking study ever published (Davidson *et al.*, 2020) gathered 15 million data points during 30 years, for 96 animal species, across land and sea in the Arctic.

The challenges of working with big tracking data

(1) Data management:

Once big data sets of tracking data for marine megafauna have been recorded, the first challenge is

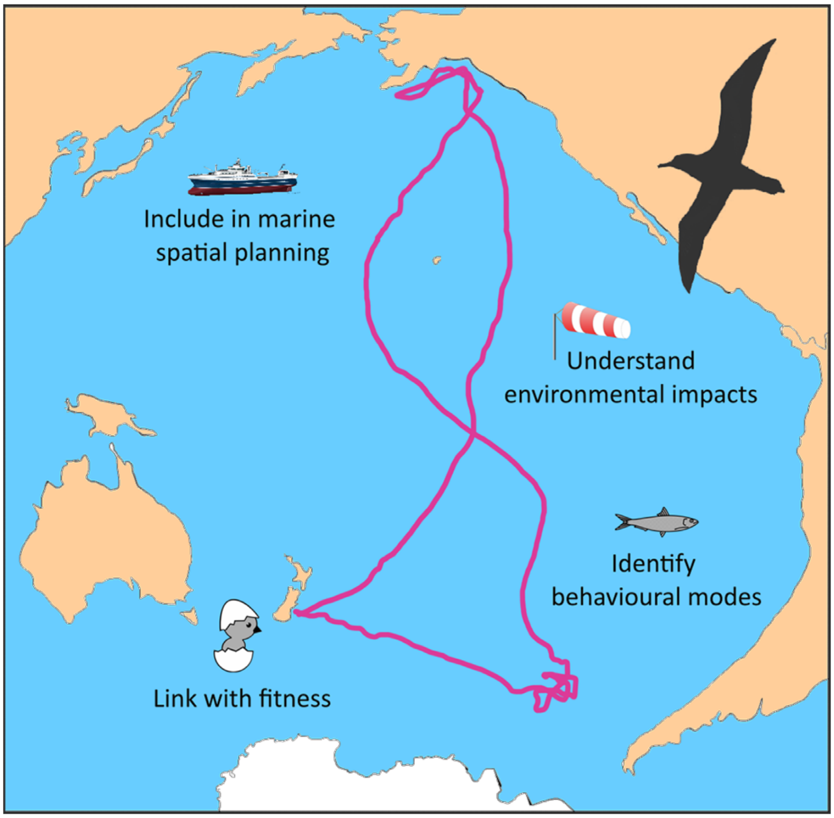

Figure 2. Imaginary example of tracking data and its use for studying the ecology and conservation of marine megafauna.

to format and store them in secure and accessible databases. This is generally not a technical problem for tracking information, and automatic uploading feature onto databases such as Movebank exist (Kranstauber *et al*., 2011). Yet other bio-logging data such as accelerometry, video, and acoustic recordings generate far larger volumes of information, and are currently more or less absent from large online databases. Also, experience has shown that efficient data curation and exchange with the scientific community does require advanced technical skills and time, making this task a full-time job in research institutions performing a lot of wildlife tracking. This challenge is enhanced when data are made available in real time, as within the program Marine Mammals Exploring the Oceans Pole to Pole, and when data sets are linked with information on the biology of studied individuals (sex, age, reproductive status, and population trends). Data curation is also demanding when tracking information is combined with the very large volumes of oceanographic data provided by satellite remote sensing by marine megafauna as samplers of their environment (McMahon *et al*., 2021), and/or by models simulating physical and biological processes (Cotté *et al*., 2015; Treasure *et al*., 2017). Consequently, research labs providing dedicated engineer positions perform much better than others, where research scientists spend a lot of their time curating big data, with little recognition from their hierarchy. This could be compensated via further dedicated work of wealthier laboratories, to create tools and provide technical support, allowing all researchers to remotely upload and share their data (e.g. the Movebank initiative).

(2) Analyses:

The second step when analysing big tracking data is to identify behavioural modes along the tracks of marine megafauna (Figure 2). Usually, this consists of filtering data to determine travelling, resting, and feeding phases. This is important, since conservation measures will differ according to these phases, with often higher levels of preservation for feeding (or breeding), then resting, and lastly for areas, animals only travel through. Initially, filtering tracking data drew its rational from previous studies on terrestrial animals, mainly insects (Bell, 1991). Those used speed and sinuosity indexes: An animal travelling fast and straight is assumed to be commuting, whereas a slower and more sinuous path is distinctive of active prey searching, and very slow motion indicates resting (Grémillet *et al*., 2004). This metric is often seen as rudimentary, yet variations along this analytical theme remain valid to this date (Andrzejaczek *et al*., 2019). First passage time (FPT) analyses were also widely used by pioneering tracking studies of marine megafauna (Pinaud and Weimerskirch, 2007), but this approach was criticized by Barraquand and Benhamou on a series of statistical grounds (Barraquand and Benhamou, 2008), and they proposed using residence time (the time spent near a location). This seemed both simple and sound, yet the method was soon supplanted by the widespread use of Bayesian approaches for the classification of behavioural modes along marine animal tracks. This is the case of hidden Markov models (HMMs) which were initially used to classify movement behaviour (Patterson *et al*., 2009) in southern bluefin tuna (*Thunnus maccoyii*), followed by more general state-space models. Those state-space approaches greatly improved the accuracy of behavioural inferences along animal tracks, and accounted for the natural temporal dependency in behaviours (Patterson *et al*., 2017). Following the landmark methodological publication by Ian Jonsen and colleagues (Jonsen *et al*., 2005), HMMs are currently the most widespread method to categorize behaviours along the tracks of marine megafauna, with constant methodological refinements (Michelot and Blackwell, 2019). Yet, associated routines require substantial computing power and long running times, which often delay analytical processes.

Analysts often tend to reinvent the wheel, and to denigrate previous work. In this context, Patterson and colleagues (Patterson *et al*., 2017) warned: "There is a trend in movement ecology toward […] overly-complex modelling approaches". The authors wisely concluded that: "Ecologists mostly […] need intuitive and practical tools which they can implement and handle themselves". This is now possible through the profusion of routines available within the R computing environment (Joo *et al*., 2020), and through simplified classification routines, such as the calculation of residence through space and time (Torres *et al*., 2017) or segmentation-clustering methods (Patin *et al*., 2020).

(3) Modelling:

Next, tracking data can be combined with other information sources (Figure 2), on (a) the behaviour and the physiology of marine megafauna, on (b) their physical and biological environments, and on (c) threats to them. This allows (d) the identification and the prediction of marine areas essential for conservation, now, and in the future.

(a) Ecophysiological information on tracked animals can be provided by bio-logging, with a great variety of sensors (Ropert-Coudert and Wilson, 2005) ranging from simple temperature probes to on-board video and acoustic recorders (Sequeira *et al*., 2021). Among them, 3D accelerometers became prominent across the last decade. These modules, which are the same as those spying on body movements in our smartphones, were initially deployed to record high-frequency ethograms of marine animals on the move (Sakamoto *et al*., 2009), but were not necessarily linked to tracking information on spatial distribution. This is now common practice through combined deployments of GPS, accelerometers, and magnetometers within the same tags, which allow the three-dimensional investigation of marine megafauna movements. Machine learning approaches are particularly useful in this regard, because large volumes of accelerometry data can be automatically and rapidly analysed (Bidder *et al*., 2014). For instance, deep learning convolutional neural networks can be used for the automatic identification of behavioural patterns from sea turtle accelerometry data (Jeantet *et al*., 2021). Those can then be verified through the combined use of cameras affixed to a subset of studied animals (Jeantet *et al*., 2020).

While GPS-tracking usually allows the identification of three major behavioural modes (travelling, foraging, and resting), accelerometry data pinpoint numerous other behavioural features, notably those linked to prey capture (Chimienti *et al*., 2016). They may also provide proxies for energy expenditure across time, through calculation of overall dynamic body acceleration (Wilson *et al*., 2006, 2020). With information available both on energy expenditure and capture yields, it is therefore possible to infer the energy balance of marine animals across time and space, and to map their energyscapes identifying areas that are particularly profitable, or unprofitable for them (Amélineau *et al*., 2018), and therefore shape their individual fitness (Grémillet *et al*., 2018b).

(b) To understand the drivers of such energyscapes, it is essential to put tracking data in the context of the biotic and abiotic environments of marine megafauna. Thereby, animal tracks are mostly linked with remote-sensed variables such as sea-surface temperature and ocean colour, depicting spatio-temporal patterns of marine productivity. This approach is useful, but might be biased by spatio-temporal mismatches between primary productivity measured at the ocean surface, and the actual three-dimensional availability of prey to marine megafauna (Grémillet *et al*., 2008). Therefore, to understand the whereabouts of top predators, it is essential to gather information on prey fields, and those may be linked to predator distributions using resource selection functions (Courbin *et al*., 2018). More generally, statistical relationships can be built between megafauna distributions and environmental variables, the most important being prey fields, followed by bathymetry. Indeed, this second feature has already been identified by pioneering studies (e.g. Garthe, 1997), and confirmed ever since for its decisive importance in shaping oceanic fronts aggregating productivity and marine megafauna (Nur *et al*., 2011; Chambault *et al*., 2017). Such fronts, which may also occur at the boundary between water masses and independently of bathymetry, are a global determinant of marine megafauna aggregations (Scales *et al*., 2014). To better identify these aggregative features, further oceanographic variables (*in situ* or modelled) can be added to statistical analyses: Sea-surface height, eddy kinetic energy, and other variables indicative of ocean currents (Scales *et al*., 2018), three-dimensional patterns of marine productivity (Saba *et al*., 2010), information on the deep-scattering layer indicative of the aggregation of mesopelagic prey (Le Croizier *et al*., 2020), oxygen concentrations and pH values pinpointing anoxic zones (Bakun *et al*., 2015), or measurements of bioluminescence indicating the presence of potential prey in the aphotic zone (Vacquie-Garcia *et al*., 2012). Importantly, some of these key variables can now be studied using additional sensors attached to foraging marine megafauna, including echosounders detecting mid-trophic levels organisms, including prey fields (Goulet *et al.*, 2019; Tournier *et al.*, 2021).

(c) Variables alluded to in the previous paragraph can fluctuate naturally, but also under the influence of human activities, causing threats to marine megafauna. Notably, climate change can affect marine productivity, because global warming transforms the spatio-temporal abundance of prey available to top predators (Cheung *et al.*, 2010). Fisheries also compete with marine megafauna on a worldwide scale (Grémillet *et al.*, 2018a), and generate global by-catch threats to large oceanic animals (Worm *et al.*, 2006). In addition, those are impacted by chemical and plastic pollutions (Kühn and Van Franeker, 2020; Albert *et al.*, 2021), marine traffic (Peltier *et al.*, 2019), and habitat loss (e.g. (Sievers *et al.*, 2019)). Indeed, big data approaches also encompass large-scale information on this series of threats generated by humanity (Kroodsma *et al.*, 2018), and on their impacts on the spatial ecology and conservation of marine megafauna (e.g. (Grose *et al.*, 2020)).

(d) Once linkages between marine megafauna, oceanographic patterns, and processes are better understood in the context of global changes, habitat models can be built. Those use statistical relationships between megafauna occurrence data and environmental features at the time and place of the investigations, to infer megafauna presence across yet unstudied areas and time-scales (Redfern *et al.*, 2006). Animal occurrence data can also be linked to population data to infer actual animal densities across marine areas (Carneiro *et al.*, 2020; Beal *et al.*, 2021). These approaches are particularly important in the context of exploited marine species (Péron *et al.*, 2016), of marine spatial planning (Sequeira *et al.*, 2019b), and of testing the incidence of different climate change scenarios (Clairbaux *et al.*, 2021a). For this purpose, general additive mixed models (GAMMs) are the most commonly used statistical tool (but see Thuiller *et al.*, 2009; Oppel *et al.*, 2012 for review and alternatives), whereby their accuracy and reliability critically depend upon the quality of environmental information linked to animal tracking data (Yates *et al.*, 2018), and of working at adequate spatio-temporal scales (Authier *et al.*, 2017). Yet, GAMMs are unlikely to cope with millions of data points, and MAXENT or other machine learning approaches might be more suitable in the future. Further, there are clear issues with the transferability of habitat models, from an ecological context into another (Péron *et al.*, 2018; Yates *et al.*, 2018). Beyond these statistical approaches, big data information on marine megafauna ecology can be also used to parametrize mechanistic models. This is notably the case of NicheMapper^{TM}, an algorithm used to simulate the energy balance of marine predators in the context of environmental variability (Clairbaux *et al.*, 2021b), but a range of other process-based ecosystem models may also benefit from distribution data for marine megafauna, notably Ecopath with Ecosim (Christensen *et al.*, 2005) and OSMOSE (Travers *et al.*, 2007). Those models are the main facilitators of marine ecosystem-based management (Heymans *et al.*, 2016).

Preserving marine megafauna using big tracking data

As acknowledged by Hyrenbach and colleagues over 20 years ago (Hyrenbach *et al.*, 2000): “Pelagic species forage far from their breeding areas and do not respect arbitrary boundaries imposed by managers.” In their seminal work on marine protected areas (MPAs) and ocean basin management, the authors pointed to the high mobility of marine megafauna, and the many challenges these movements created for marine spatial planning and conservation. Their synthesis was soon echoed by an equally fundamental review compiled by Hooker and Gerber (Hooker and Gerber, 2004), on marine reserves in the context of marine megafauna. Both writings underlined the importance of gathering detailed knowledge on the whereabouts of large marine animals, implicitly pointing to the value of global tracking data for these species. Indeed, big tracking data accumulated across the last two decades opened worlds of knowledge on the spatial ecology of marine megafauna (Figure 3). It notably helped identify areas irreplaceable for species conservation (Grémillet *et al.*, 2014) and multi-species hotspots (Grecian *et al.*, 2016). From a legal perspective, those track-based protection areas notably take the form of Ecologically or Biologically Significant Areas (EBSAs), of Essential Fish Habitats (EFHs), of Important Bird and Biodiversity Areas (IBAs), and of Important Marine Mammal Areas (IMMAs) (Hays *et al.*, 2019). Multispecies tracking of marine birds and mammals, thereby led to the designation of MPAs, one of the first and largest of its kind, covering 665301 km^2 in the Southern Ocean (Delord *et al.*, 2014). Despite these spectacular advances, tracking-based MPAs faced two major challenges. First, even though Hyrenbach and colleagues called for mobile MPAs, most MPAs are static, of limited extent, and they are primarily defined using benthic criteria, rather than information on highly mobile megafauna. Therefore, their value for oceanic species might be questioned (Hyrenbach *et al.*, 2000). Yet, detailed investigations revealed that even coastal MPAs fit well with the distribution zones of some mobile predators, at least during the reproduction phase, during which they function as central-place foragers (Péron *et al.*, 2013; Hays *et al.*, 2021). Second, the actual benefits of MPAs for marine megafauna remained initially unclear, even though early GPS-tracking studies within fishery exclusion zones did demonstrate more or less immediate benefits (Pichegru *et al.*, 2010).

Overall, despite thousands of tracking studies, conservation benefits often seem meagre, and one of the key questions in marine megafauna movement ecology remains: “How can movement data be used to support conservation and management?” (Hays *et al.*, 2016). After raising this issue, Hays and colleagues adequately answered it by detailing 34 success stories around the world, within which tracking information on seabirds, marine mammals, turtles, and fish were used for effective conservation action in favour of these species, and of the marine environment (Hays *et al.*, 2019). The authors acknowledge the potential biases of their expert team in collecting these studies, and hence many more may exist, such as the recent designation of the MPA in the Ross Sea (Brooks *et al.*, 2020). Also, in the meantime, a major multi-species tracking study has been released for the marine region

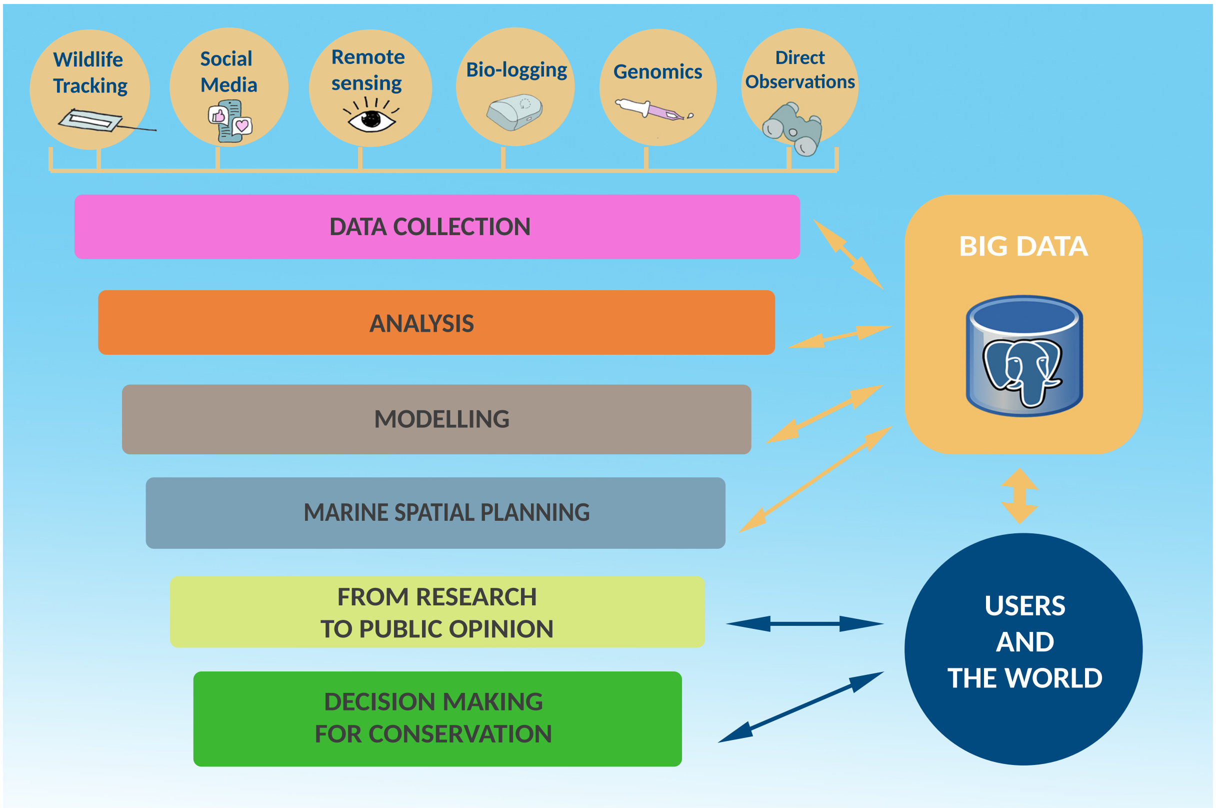

Figure 3. Working for conservation with big data on the spatial ecology of marine megafauna.

bordering Antarctica (Hindell *et al.*, 2020). This analysis integrated >4000 tracks from 17 birds and mammal species, to identify areas of ecological significance around the sub-Antarctic islands of the Atlantic and of the Indian Ocean, as well as over the Antarctic continental shelf. As these areas are under the combined stressors of climate change and fisheries, tracking information will be essential to the designation of new MPAs across these vast regions, notably under the auspices of the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR). Even more remarkably, Davies and colleagues (Davies *et al.*, 2021) used tracking data, along with information on population numbers and phenology for 21 seabird species breeding all across the Atlantic ocean, to identify a major year-round hotspot associated with the subpolar frontal zone of the North Atlantic. They demonstrated that this specific area aggregated between 2.9–5 million seabirds from at least 56 colonies, and their analysis led to the designation of this ca. 600000 km^2 as an MPA by the OSPAR commission.

Yet, the way from tracking to actual conservation benefits for marine megafauna, is often an extremely long one (Hays *et al.*, 2019; see their six-step flow chart). It might also be a highly frustrating process for scientists, who rightly think that they are not being heard, that only a fraction of their recommendations are being implemented, and that "paper parks" with only weak legislation and surveillance are being created (Meehan *et al.*, 2020). For example, the Ross Sea MPA only covers one-eighth of the area initially identified as irreplaceable for the ecological functioning of the "Last Ocean" (Brooks *et al.*, 2020).

The way forward

As Authier and colleagues rightly stated: "Marine megafauna provides in fact a striking and concrete illustration of the synergistic interplay between technological innovations and advanced modelling. This synergy opens the door to ecosystem-based management which is the cornerstone of current conservation policies" (Authier *et al.*, 2017). Indeed, the potential for using big data to address the spatial ecology and the conservation of marine megafauna has never been so high, and is ever expanding. Data volumes thereby grow super-exponentially, because the memory size per gram of biologger doubles every 2 years (Elliott, 2016), because of the multiplicity of new sensors that can be fitted to biologgers, and because the 1000 remote-sensing satellites that are currently operating generate >100 terabytes of data per day (Amani *et al.*, 2020). As dozens of satellites can now be launched within single missions, this super-exponential growth in data availability is bound to persist, augmented by the wealth of information provided by human social media (Thums *et al.*, 2018).

Wading through these terabytes of data is a methodological challenge, but Sequeira and colleagues provided a roadmap, notably for advanced standardization of bio-logging data, with an emphasis on data sharing and open access (Sequeira *et al.*, 2021). Such standardization, which should ideally be promoted by tag manufacturers and users alike, will make tracking data available in near real-time (Navarro *et al.*, 2016), with their automatic transfer to global, open access databases (reviewed in (Sequeira *et al.*, 2019b, 2021)). Also, it seems essential to share expertise, with publically accessible platforms for posting analytical routines, such as GitHub. Analysed spatial information can then contribute to global initiatives such as the Marine Megafauna Movement Analytical Program (MegaMove) and the Global Ocean Observing System, for dynamic marine spatial planning and a better protection of marine biodiversity, not only within coastal areas encompassed within exclusive economic zones, but also in high seas beyond national jurisdictions. In practice, the aim of such global initiatives is to generate freely accessible, dynamic, and interactive maps overlaying global threats generated using automated detection algorithms, to the trajectories and distributions of marine megafauna (Sequeira *et al*., 2019b).

Yet, beyond what might be perceived as a technological race forward, it also seems important for our research community to occasionally stand back and reflect on the ethical (Reduce–Refine–Replace framework, see Richmond, 2000), environmental (environmental footprint, see Grémillet, 2008), and societal implications of using big data to study the spatial ecology and conservation of marine megafauna. It thereby appears that, on a worldwide scale, most big tracking studies are still conducted in an uncoordinated manner (but see notable exceptions such as the Ocean Tracking Network, MegaMove, and Icarus). Hence, beyond the temptation to simply "track all marine animals", it seems essential to always carefully determine necessary sample sizes according to the potential impact of tagging on sensitive species, to biases linked to the choice of sites at which individuals are tagged (O'Toole *et al*., 2021), and to the statistical power required to run specific analyses (Sequeira *et al*., 2019a). Further, now is also the time to run gap analyses using existing tracking information. This has been performed by Bernard and colleagues (Bernard *et al*., 2021) for the world seabird community, and they showed that even though this group has been subjected to at least 700 tracking studies on >28000 individuals, key movement information is still lacking for 54 threatened species, notably in tropical areas. Such knowledge led the authors to call for an ethically, environmentally, and logistically sound global initiative for seabird tracking, which could be expanded to the world's marine megafauna.

But producing knowledge on the spatial ecology of marine megafauna is only one step towards their conservation (Hays *et al*., 2019). From there, how do we make decision-makers aware of research findings, and motivate them to take decisions in favour of marine nature protection? This is currently the key issue, which expands to the entire biosphere, and will not be solved through the production and use of big data alone. As the general public is generally fascinated both by charismatic megafauna and by electronic technologies, animal bio-logging has a strong potential for winning people's attention (Lescroël *et al*., 2016). Nevertheless, publishing in scientific journals, on websites, or in conventional media is not sufficient any more. Especially when communicating with younger generations, posting of images, animations, videos on social media, and the use of virtual reality systems seem far more likely to have an incidence on public opinion, and politicians strongly respond to fast-track media (Kalsnes *et al*., 2017). Therefore, for the coming generation of conservation biologists, the major challenge will be to make research findings visible on social media through collaborations with communication and virtual reality specialists, while safeguarding scientific objectivity and integrity, and keeping in mind the environmental footprint of big data science.

Data availability statement

No new data were generated or analysed in support of this research.

Author contributions

DG performed and wrote this review, to which DC and CG contributed.

Conflict of Interest statement

None

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