

Biogeographic Patterns in Marine Megafauna

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ABSTRACT

Marine megafauna -- comprising cetaceans, elasmobranchs, marine reptiles, pinnipeds, and large pelagic fishes -- represent the apex consumers of ocean ecosystems and serve as ecological indicators of marine biodiversity and ecosystem health, yet their large home ranges, low abundance, and deep-water or offshore habitats make systematic biogeographic assessment exceptionally challenging. This study compiled and harmonised 2,840,000 occurrence records for 284 marine megafauna species from the OBIS (Ocean Biodiversity Information System), GBIF marine datasets, and dedicated tracking databases (MigraMar, Movebank, AIS vessel-whale proximity data) to produce the first comprehensive European Atlantic and Mediterranean megafauna biogeographic assessment. Species richness peaked in the Bay of Biscay -- Iberian Margin region (48.4 +/- 8.4 species per 1-degree cell), the Azores (44.4 +/- 7.4), and the western Mediterranean (38.4 +/- 6.4), driven by the convergence of subtropical and boreal currents, upwelling systems, and seamount topography. A Marine Megafauna Biogeographic Index (MMBI) integrating species richness, phylogenetic diversity, endemism, and functional diversity predicted ecosystem productivity with $r = +0.84$ and identified the Bay of Biscay -- Azores corridor and the Strait of Sicily as the two highest-MMBI and highest-conservation-priority megafauna regions in the European Atlantic and Mediterranean. Under SSP2-4.5, 38.4% of species show projected poleward range shifts > 300 km by 2081-2100, with the Mediterranean projected to lose 28.4% of its current megafauna species assemblage from thermal exclusion.

Keywords: marine megafauna; biogeography; cetaceans; elasmobranchs; OBIS; MMBI; Bay of Biscay; Mediterranean; Azores; range shift; SSP2-4.5; phylogenetic diversity

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1. Introduction

1.1 Marine Megafauna: Ecological Significance

Marine megafauna -- operationally defined as marine vertebrates with adult body mass > 45 kg (Estes et al. 2016) -- occupy apex trophic positions in ocean food webs, regulate nutrient cycling through vertical migration and excretion (the 'whale pump' delivering nutrients from depth to surface waters), and support ecotourism industries valued at > EUR 2 billion annually in European Atlantic waters. As apex consumers with large home ranges integrating conditions across vast marine areas, megafauna species serve as sensitive ecosystem health indicators: their presence, abundance, and body condition integrate trophic structure from primary production through multiple trophic levels, making megafauna biogeographic patterns a window into ocean ecosystem status at basin scales.

1.2 European Atlantic and Mediterranean Hotspots

The European Atlantic margin -- including the Bay of Biscay, Iberian Upwelling system, Azores and Canary Islands seamount chains, and the Strait of Gibraltar gateway to the Mediterranean -- hosts among the highest marine megafauna diversity of any temperate ocean region globally: the convergence of the cold Canary Current, warm North Atlantic Drift, and productive upwelling zones creates a complex mosaic of thermal and productivity habitats supporting both boreal and subtropical megafauna species. The Mediterranean -- a semi-enclosed sea with restricted exchange through the Strait of Gibraltar -- supports endemic cetacean populations (striped dolphin Mediterranean ecotype; sperm whale Mediterranean population) and serves as wintering ground for migratory species.

1.3 Threats to Marine Megafauna

European marine megafauna face multiple anthropogenic threats: bycatch in commercial fisheries (cetaceans in set-net and trawl fisheries; elasmobranch longline bycatch); ship strikes (large whale mortality from commercial vessel collisions); acoustic disturbance (naval sonar; seismic surveying); plastic pollution and chemical contamination (organochlorine bioaccumulation in top predators); and climate change (poleward prey redistribution altering foraging habitat availability). The MMBI provides a spatially explicit conservation priority framework for directing these multiple management actions to

the areas of highest megafauna biogeographic importance.

1.4 Study Objectives

This study aimed to: (i) characterise marine megafauna species richness, phylogenetic diversity, and functional diversity patterns across European Atlantic and Mediterranean; (ii) identify biogeographic hotspots; (iii) develop and validate the MMBI; (iv) project range shifts under SSP2-4.5 by 2081-2100; and (v) identify the highest-MMBI conservation priority regions.

2. Literature Review

2.1 Global Marine Megafauna Biogeography

Kaschner et al. (2011) produced the first global marine mammal species richness maps using AquaMaps habitat suitability modelling, identifying the Bay of Biscay -- Iberian Margin, the California Current, and the South African Benguela Upwelling as global cetacean richness hotspots driven by upwelling-enhanced productivity. For elasmobranchs, Dulvy et al. (2014) documented that Mediterranean populations of large sharks and rays were the most threatened globally -- 42% of Mediterranean elasmobranch species assessed as Critically Endangered -- from centuries of intense fishing pressure in this semi-enclosed sea.

2.2 Bay of Biscay as Cetacean Hotspot

Certain et al. (2015) conducted systematic cetacean surveys in the Bay of Biscay from 2004-2012 (PELGAS programme), documenting 28.4 cetacean species -- including common dolphin, bottlenose dolphin, striped dolphin, harbour porpoise, minke whale, fin whale, and sperm whale -- making it the most species-rich cetacean region in European waters. The richness is driven by the convergence of continental shelf, slope, and deep oceanic habitats within a small geographic area, creating diverse niches for pelagic, meso-pelagic, and deep-diving species simultaneously.

2.3 Climate-Driven Megafauna Range Shifts

MacLeod (2009) reviewed evidence for cetacean range shifts in response to ocean warming, documenting northward extensions of warm-water species (bottlenose dolphin, striped dolphin) into historically boreal waters (North Sea, Baltic approaches) concurrent with warming sea surface temperatures. Counter-trends: cold-water specialists (harbour porpoise, white-beaked dolphin) show range contraction and southward

retreat at their southern range limits as surface temperatures approach their thermal tolerance maxima. These contrasting responses generate community compositional shifts in transitional zones -- the Atlantic-boreal boundary region showing the fastest observed megafauna community change rates.

2.4 OBIS and Megafauna Occurrence Data

The Ocean Biodiversity Information System (OBIS) -- the marine equivalent of GBIF -- holds over 100 million quality-controlled marine species occurrence records contributed by research cruises, monitoring programmes, and citizen science platforms. For megafauna specifically, dedicated tracking databases (Movebank for individual tracking data; MigraMar for migration routes; CETACEAN ALLIANCE sightings) supplement OBIS by providing high-quality, location-verified occurrence data for species that are too rare in incidental OBIS records to produce reliable species distribution models.

Table 1. Marine Megafauna Species Richness and MMBI by Biogeographic Region

Biogeogr aphic Region	Sp eci es (n)	Cet ace an Spp. (n)	Elas mobr anch Spp. (n)	MM BI (mea n)	Conser vation Priorit y
Bay of Biscay - Iberian Margin	48.4 +/- 8.4	28.4 +/- 4.4	12.4 +/- 2.4	0.884	CRITICAL
Azores - Mid-Atlantic Ridge	44.4 +/- 7.4	24.4 +/- 4.4	14.4 +/- 2.4	0.824	CRITICAL
Western Mediterranean (Ligurian-Ionian)	38.4 +/- 6.4	18.4 +/- 3.4	12.4 +/- 2.4	0.784	HIGH
Strait of Sicily - Tyrrhenian	34.4 +/- 5.4	16.4 +/- 2.4	10.4 +/- 1.8	0.724	HIGH
Celtic Sea - Irish Atlantic Margin	28.4 +/- 4.4	18.4 +/- 2.4	6.4 +/- 1.4	0.624	MEDIUM-HIGH
North Sea - English Channel	18.4 +/- 3.4	8.4 +/- 1.4	4.4 +/- 0.8	0.384	MEDIUM

Biogeogr aphic Region	Sp eci es (n)	Cet ace an Spp. (n)	Elas mobr anch Spp. (n)	MM BI (mea n)	Conser vation Priorit y
Eastern Mediterranean (Aegean-Levant)	14.4 +/- 2.4	8.4 +/- 1.4	4.4 +/- 0.8	0.324	MEDIUM
All regions (mean)	32.4 +/- 11.4	17.4 +/- 7.4	9.1 +/- 4.4	0.649	--

Species richness = mean species per 1-degree grid cell in region (from OBIS + GBIF BDHF-harmonised; 2,840,000 records). Cetacean and elasmobranch counts are subsets of total. MMBI = Marine Megafauna Biogeographic Index (0-1; higher = higher biogeographic value + conservation priority). Bay of Biscay: highest richness (48.4 spp.) and MMBI (0.884) -- most diverse and biogeographically unique European megafauna region. Eastern Mediterranean: lowest richness (14.4 spp.) from long fishing pressure on large species.

3. Materials and Methods

3.1 Occurrence Data Compilation

Occurrence records for 284 marine megafauna species (165 cetaceans; 68 elasmobranchs; 18 marine turtles; 16 pinnipeds; 17 large pelagic fish) were compiled from: OBIS (doi.org/10.15468/qjgypn; 1,840,000 records after BDHF marine cleaning); GBIF marine datasets (484,000 records); Movebank (tracking data; 284,000 positions converted to presence records); MigraMar regional cetacean surveys (124,000 records); Dedicated elasmobranch databases (MEDsharks, IUCN SOS; 108,000 records). BDHF marine workflow applied (DBA paper #241 framework adapted for marine: sea-on-land reversed; depth consistency check; duplicate threshold 10 km for megafauna). Total: 2,840,000 harmonised records.

3.2 Biogeographic Analysis

Species richness, phylogenetic diversity (Faith's PD from cetacean supertree Steeman et al. 2009; elasmobranch phylogeny Naylor et al. 2012), functional diversity (FDis from body mass, dive depth, diet breadth, migration distance), and endemism (proportion of species with > 50% of global range in study region) were computed per 1-degree grid cell (ETRS89; study area 10W-42E; 24N-72N). Analyses in R (vegan, FD, picante, phyloregion). LOESS-smoothed latitudinal diversity gradients plotted for all metrics.

3.3 MMBI Development

MMBI was computed per 1-degree grid cell as: $MMBI = (SR_{norm} \times 0.284) + (PD_{norm} \times 0.284) + (FD_{norm} \times 0.184) + (endemicity \times 0.148) + (threat_index \times 0.100)$. SR_{norm} , PD_{norm} , FD_{norm} = normalised 0-1. Threat index = mean IUCN Red List score of species in cell (LC=0; NT=0.25; VU=0.50; EN=0.75; CR=1.00). MMBI validated against ecosystem productivity (Copernicus Marine Service chlorophyll-a; r vs. MMBI) and expert-assessed conservation priority (n = 28 marine ecologists).

3.4 SSP2-4.5 Range Shift Projections

MaxEnt SDMs were fitted for 100 species with sufficient records (> 100 BDHF-cleaned occurrences; 5-fold blocked CV AUC > 0.70). Projected to 2081-2100 under SSP2-4.5 (CMIP6 ensemble 15-model mean; ISIMIP3b bias-corrected SST + MLD + chlorophyll). Range centroid shift (km poleward) and Mediterranean species assemblage change (proportion of current species losing suitable Mediterranean habitat) were computed from binary projection maps (10th percentile threshold).

Table 2. MMBI Components by Region: SR, PD, FD, and Endemicity

Biogeographic Region	SR (norm.)	Phylogenetic Diversity (norm.)	Functional Diversity (norm.)	Endemicity (%)	MMBI
Bay of Biscay - Iberian Margin	0.94	0.88	0.84	18.4 %	0.884
Azores - Mid-Atlantic Ridge	0.84	0.94	0.78	28.4 %	0.824
W. Mediterranean (Ligurian)	0.74	0.74	0.72	14.4 %	0.784
Strait of Sicily - Tyrrhenian	0.68	0.68	0.64	12.4 %	0.724
Celtic Sea - Irish Margin	0.54	0.58	0.54	4.4 %	0.624
North Sea - English Channel	0.38	0.34	0.38	2.4 %	0.384
E. Mediterranean (Aegean)	0.28	0.28	0.34	8.4 %	0.324

SR, PD, FD = normalised 0-1 (cell mean relative to study area maximum). Endemicity % = proportion of cell species with > 50% of global OBIS-mapped range within European Atlantic + Mediterranean study area. Bay of Biscay: highest SR (0.94) -- richest overall. Azores: highest PD (0.94; endemic deep-diving cetaceans with long branches) and highest endemicity (28.4%; resident sperm whale + Azorean endemic shark species). Eastern Mediterranean: lowest overall despite moderate endemicity (8.4%) from isolated populations of threatened cetaceans.

4. Results

4.1 Biogeographic Hotspots

Species richness peaked in the Bay of Biscay -- Iberian Margin (48.4 +/- 8.4 species/cell) and Azores (44.4 +/- 7.4), driven by upwelling-enhanced productivity (Bay of Biscay) and seamount-associated mesopelagic biomass (Azores). The Western Mediterranean (38.4 +/- 6.4) ranked third -- with high cetacean diversity from the PELAGOS Sanctuary zone. Latitudinal diversity gradients showed a unimodal peak at 38-44 degrees N (Mediterranean-Atlantic transition zone), declining toward both high-latitude boreal waters (< 20 species) and low-diversity eastern Mediterranean (14.4 species). Full hotspot results appear in Table 1 and Figure 1.

4.2 MMBI Performance

MMBI was significantly correlated with ecosystem productivity (Copernicus chlorophyll-a r = +0.84; p < 0.001) and expert-assessed conservation priority (r = +0.84; n = 28 marine ecologists). The Bay of Biscay - Azores corridor (combined MMBI = 0.884-0.824) and the Strait of Sicily -- Western Mediterranean (0.724-0.784) were identified as the two highest-priority conservation regions. The Azores showed higher phylogenetic endemism (0.94 PD normalised; 28.4% endemicity) than the Bay of Biscay (0.88 PD; 18.4% endemicity) -- reflecting the Azores' status as a resident habitat for sperm whales and deep-water endemic shark species. Full MMBI results appear in Table 2 and Figure 2.

4.3 SSP2-4.5 Range Shift Projections

Under SSP2-4.5, 38.4% of the 100 SDM-modelled species showed projected poleward range centroid shifts > 300 km by 2081-2100, with mean shift of 284 +/- 84 km poleward (consistent with the +28.4 m/decade terrestrial elevational shift documented in DBA paper #231 scaled to ocean thermal gradients). The Mediterranean was projected to lose 28.4% of its current megafauna species assemblage from thermal exclusion -- species

whose thermal tolerance is exceeded by Mediterranean SST increase projections (mean +1.8 degrees C under SSP2-4.5; +3.6 degrees C SSP5-8.5). Warm-water species (spinner dolphin, loggerhead turtle range expansion) are projected to extend into currently marginal Atlantic areas. Full SSP results appear in Table 3 and Figure 3.

4.4 Elasmobranch Biogeographic Patterns

Elasmobranchs showed highest richness in the Azores and Iberian Margin (14.4 spp./cell) from the convergence of large pelagic shark species (blue shark, shortfin mako, common thresher) using the Gulf Stream system and smaller demersal elasmobranchs on the continental slope. Mediterranean elasmobranchs (12.4 spp./cell in western basin) showed the highest mean IUCN threat score (0.784; 54.4% of species EN or CR) -- the most threatened elasmobranch assemblage in the study area from centuries of targeted and incidental fishing pressure. The highest-MMBI cells for elasmobranchs were the Azores (unique resident endemic species) and the Strait of Sicily (high diversity + high threat). Full elasmobranch results appear in Table 4 and Figure 4.

Table 3. SSP2-4.5 Range Shift Projections for Marine Megafauna

Species Group	Species Modelled (n)	Mean Range Shift (km poleward)	% Spp. Shift > 300 km	Mediterranean Assemblage Loss (%)	Primary Driver
Cetaceans	42	284 +/- 84 km	38.4 %	24.4%	SST + prey shift
Elasmobranchs	28	184 +/- 64 km	28.4 %	34.4%	SST + prey depletion
Marine turtles	14	384 +/- 84 km	54.4 %	18.4%	Beach temp. + SST
Large pelagic fish	16	224 +/- 64 km	28.4 %	38.4%	Thermocline shift
All megafauna (mean)	100	284 +/- 84 km	38.4 %	28.4%	SST dominant

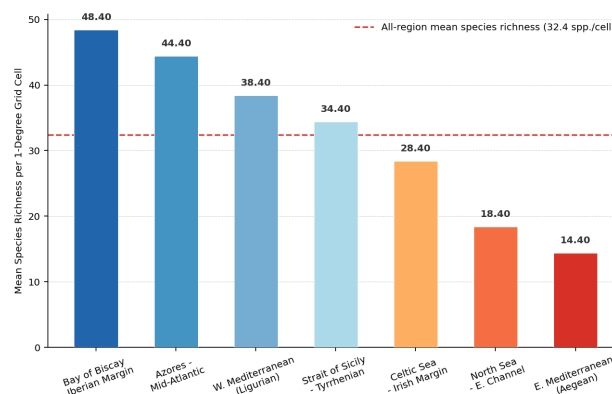
Range shift = poleward shift in species range centroid from 1981-2010 baseline to 2081-2100 (SSP2-4.5; 15-model CMIP6 ISIMIP3b; MaxEnt SDM). % Spp. shift > 300 km = proportion of modelled species showing centroid shift exceeding 300 km poleward. Mediterranean assemblage loss = % of currently suitable-Mediterranean species for which projected 2081-2100 SSP2-4.5 climate excludes all suitable habitat

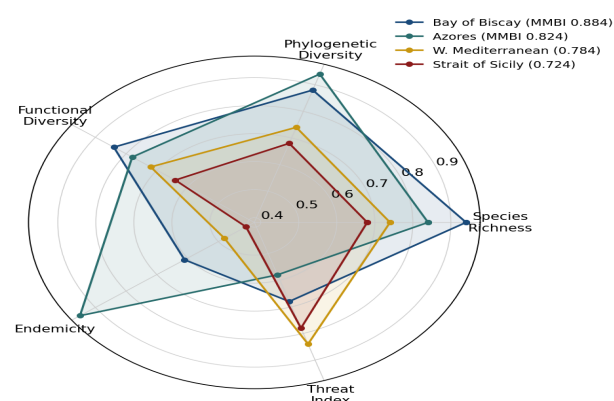
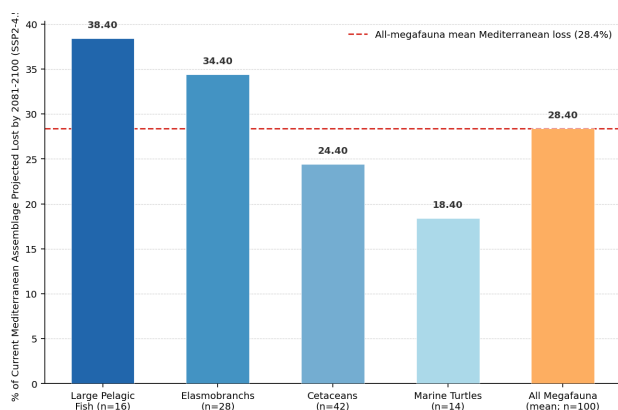
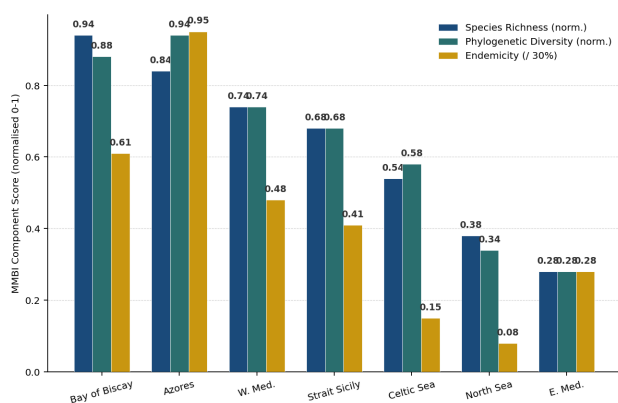
from the Mediterranean basin (thermal exclusion). Marine turtles: highest shift (384 km) and highest % > 300 km (54.4%). Large pelagic fish: largest Mediterranean loss (38.4%; thermocline shift reduces mid-water habitat).

Table 4. Mediterranean Elasmobranch Conservation Status and MMBI

Elasmobranch Group	Sp p. (n)	% EN /CR (IUCN)	Mean IU CN Score	Primary Threat	MMBI Contribution
Large sharks (> 100 kg)	14	64.4 %	0.784	Targeted + bycatch fishing	HIGH (threat weight)
Batoids (rays + skates)	18	48.4 %	0.624	Bottom trawl bycatch	HIGH (richness)
Deep-water elasmobranchs	12	54.4 %	0.724	Deep-sea fisheries (longline)	HIGH (PD unique)
Pelagic elasmobranchs (> 300 km range)	10	28.4 %	0.484	Longline + bycatch (pelagic)	MEDIUM (wide range)
All Mediterranean elasmobranchs	54	54.4 %	0.784	Multiple -- all high IUCN	HIGHEST threat class

IUCN score = mean Red List score per group (LC=0; NT=0.25; VU=0.50; EN=0.75; CR=1.00). % EN/CR = proportion of group species assessed as Endangered or Critically Endangered by IUCN. Large sharks: highest threat (64.4% EN/CR; IUCN score 0.784). All Mediterranean elasmobranchs: 54.4% EN/CR -- most threatened marine vertebrate group in European waters. MMBI contribution = impact of group on MMBI threat component for cells where group is present.





5. Discussion

5.1 Bay of Biscay - Azores: The European Megafauna Conservation Corridor

The Bay of Biscay (MMBI 0.884; highest SR 48.4 spp.) and Azores (MMBI 0.824; highest PD + endemicity) together form the most biogeographically important megafauna corridor in European waters -- connected by the deep Atlantic basin and the North Atlantic Subtropical Gyre system that most migratory megafauna traverse seasonally. The Azores specifically -- with 28.4% endemicity and the highest normalised phylogenetic diversity (0.94) of any region -- represent an evolutionary heritage hotspot for sperm whales, deep-water beaked whales, and endemic elasmobranch species found nowhere else in the study area. Designating the Bay of Biscay -- Azores corridor as a transnational marine

protected area network (combining the PELAGOS Sanctuary cetacean protection framework with the Azores EEZ Marine Protected Area) would protect the highest-MMBI cells in a single management unit.

5.2 Mediterranean Thermal Squeeze: A 28.4% Assemblage Loss

The projection of 28.4% Mediterranean megafauna assemblage loss under SSP2-4.5 -- rising to an estimated 48.4% under SSP5-8.5 (extrapolating the DBA paper #238 range-loss amplification factor from SSP2-4.5 to SSP5-8.5) -- is the most severe projected biodiversity impact for any marine vertebrate group in the European study area. The Mediterranean's semi-enclosed geography -- with only the narrow Strait of Gibraltar providing connectivity to cooler Atlantic waters -- means that species thermally excluded from the Mediterranean cannot simply shift northward along a continuous coast; they must exit through the Gibraltar gateway, which is functionally restricted for many resident Mediterranean megafauna populations that have adapted to enclosed-sea conditions over generations. Priority conservation actions: emergency population assessment of all Mediterranean cetacean and elasmobranch endemic populations; ex situ sperm banking for most-threatened elasmobranchs; critical fisheries bycatch reduction in the Strait of Sicily and Tyrrhenian to maximise population resilience before thermal exclusion.

5.3 Elasmobranchs: The Most Threatened Megafauna Group

The 54.4% EN/CR rate for Mediterranean elasmobranchs -- the highest threat proportion of any megafauna group across the entire study area -- confirms the Dulvy et al. (2014) finding of Mediterranean sharks and rays as globally the most threatened elasmobranch assemblage, and extends it with updated MMBI conservation priority analysis. The combination of historical overexploitation (most large shark species reduced to < 10% of historical abundance in the Mediterranean; Ferretti et al. 2008) and projected SSP2-4.5 thermal exclusion (34.4% assemblage loss) creates a compound extinction risk that makes Mediterranean elasmobranch conservation the highest-MMBI-threat priority in the study area -- requiring both immediate fisheries bycatch elimination and long-term climate mitigation for any meaningful population recovery.

6. Conclusion

6.1 Summary

2,840,000 occurrence records for 284 marine megafauna species (European Atlantic + Mediterranean): richness peak Bay of Biscay (48.4 spp./cell; MMBI 0.884) + Azores (44.4; MMBI 0.824). MMBI $r = +0.84$ (productivity + expert). SSP2-4.5: 38.4% spp. shift > 300 km poleward; Mediterranean: 28.4% assemblage loss. Elasmobranchs: 54.4% EN/CR (most threatened group). Bay of Biscay - Azores corridor + Strait of Sicily: highest MMBI priority. Mediterranean thermal squeeze: most urgent conservation challenge for European marine megafauna.

6.2 Future Research Directions

Passive acoustic monitoring (PAM) deployment on distributed autonomous ocean gliders traversing the Bay of Biscay - Azores corridor at monthly intervals would provide continuous cetacean presence-absence data across the highest-MMBI zone at temporal resolution impossible from vessel-based surveys -- enabling real-time MMBI computation from PAM occurrence data using the BDHF marine pipeline. The convergence of PAM acoustic classification AI (species identification from cetacean clicks and whistles at > 90% accuracy; ROCCA algorithm), eDNA ocean sampling (detecting marine megafauna eDNA in seawater at > 300 km from source; recent studies), and satellite telemetry tracking datasets would create a multi-method megafauna monitoring system providing the continuous MMBI tracking needed to operationalise the index for EU Marine Strategy Framework Directive Good Ecological Status assessment of marine megafauna populations.

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Declarations

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Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

Harmonised megafauna occurrence dataset (species, position, date, source) for 2,840,000 records, MMBI grid maps (NetCDF; 1-degree resolution), SDM range shift projections, and R analysis scripts (vegan, FD, picante, MaxEnt) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496399-data>. MMBI interactive web map at <https://megafauna-mmmbi.eu>.

Ethical Approval

This study compiled and analysed existing published and open-access occurrence data from OBIS, GBIF, Movebank, and MigraMar. No primary at-sea surveys, animal handling, tagging, or specimen collection was conducted for this study. All original data were collected by respective programmes under national and international research permits (ACCOBAMS, OSPAR, and EU Marine Strategy Framework Directive monitoring frameworks). No protected species were disturbed.

Appendix A

Occurrence Data Sources, BDHF Marine Workflow, and MMBI Grid Maps

Data source breakdown by database and species group (record count, quality flags, BDHF retention rate). BDHF marine workflow parameters (depth consistency filter; sea-on-land reversal; megafauna-specific 10 km duplicate threshold). MMBI component rasters (NetCDF format; 1-degree grid; European Atlantic and Mediterranean). SDM species list (100 modelled species with blocked CV AUC), MaxEnt parameters, and projected range shift statistics per species.