

# Satellite Telemetry in Marine Megafauna

Andreas Novak<sup>1</sup>, Nina Bianchi<sup>2</sup>

<sup>1</sup> Postdoctoral Researcher, Institute of Intelligent Systems, Swiss Institute of Machine Intelligence, Zurich, Switzerland.

Email: andreas.novak643@gmail.com | ORCID: 8115-6468-3890-7677

<sup>2</sup> Senior Lecturer, Institute of Intelligent Systems, Central European Tech University, Vienna, Austria. Email:

nina.bianchi293@gmail.com | ORCID: 1355-1355-1389-8934

## ABSTRACT

Satellite telemetry has transformed the study of marine megafauna movement ecology, enabling continuous tracking of large-bodied oceanic vertebrates across ocean basins, identifying critical foraging and breeding habitats, quantifying exposure to anthropogenic threats, and informing the spatial design of marine protected areas. This study presents a multi-species comparative analysis of satellite telemetry datasets from 847 tagged individuals across eight marine megafauna taxa -- blue whale (*Balaenoptera musculus*), leatherback sea turtle (*Dermochelys coriacea*), whale shark (*Rhincodon typus*), great white shark (*Carcharodon carcharias*), loggerhead sea turtle (*Caretta caretta*), northern elephant seal (*Mirounga angustirostris*), wandering albatross (*Diomedea exulans*), and southern bluefin tuna (*Thunnus maccoyii*) -- tracked over a cumulative 14,847 tracking days. Home range sizes (95% kernel utilisation distribution) ranged from 84,200 km<sup>2</sup> (elephant seal foraging excursion) to 47.4 million km<sup>2</sup> (wandering albatross annual range). Inter-individual movement consistency within species -- quantified as the intraclass correlation of daily displacement distance -- averaged 0.64 ± 0.18, indicating substantial but incomplete individual specialisation in space use. Anthropogenic threat hotspot analysis revealed that 68.4% of tracked blue whale core habitat (50% KUD) overlapped with high-intensity commercial shipping lanes, and 47.2% of leatherback turtle foraging areas overlapped with longline fishing effort exceeding 1,000 hooks/km<sup>2</sup>/year. Biological oceanographic drivers -- sea surface temperature, chlorophyll-a concentration, and mixed layer depth -- collectively explained 74.2% of variance in blue whale habitat use via habitat suitability modelling. These results highlight both the power of satellite telemetry for conservation-relevant spatial ecology and persistent data gaps requiring expanded tagging programmes in under-monitored ocean regions.

**Keywords:** satellite telemetry; marine megafauna; movement ecology; kernel utilisation distribution; habitat suitability; shipping lane overlap; conservation planning; biologging

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## 1. Introduction

### 1.1 Marine Megafauna and the Scale of Movement

Marine megafauna -- the large-bodied, wide-ranging vertebrates of the open ocean including cetaceans, elasmobranchs, marine turtles, pinnipeds, seabirds, and large pelagic fish -- undertake some of the most extraordinary long-distance movements in the animal kingdom, crossing ocean basins between feeding and breeding grounds, performing deep vertical dives to exploit benthic and mesopelagic prey, and navigating transoceanic migration routes with remarkable navigational precision (Block et al., 2011; Hays et al., 2016). These wide-ranging movements create acute conservation challenges: megafauna populations cross national exclusive economic zones and international high seas, encounter spatially and temporally variable anthropogenic threats including ship strikes, bycatch, noise pollution, and climate-driven prey redistribution, and require international governance frameworks that are aligned with actual space use rather than political boundaries (Maxwell et al., 2013; Hazen et al., 2018). Understanding where these animals go, why, and what threatens them en route is therefore not merely an academic pursuit but a prerequisite for effective ocean conservation.

### 1.2 Satellite Telemetry Technology and Data Products

The development of Argos satellite-linked platform transmitter terminals (PTTs) in the 1980s, followed by GPS-enabled smart position-only tags (SPOTs) in the 2000s, and most recently by miniaturised multi-sensor biologgers combining GPS, accelerometry, depth sensing, and oceanographic data recording, has produced an exponentially growing repository of marine megafauna tracking data (Hussey et al., 2015; Rutz and Hays, 2015). Analytical frameworks for converting raw location data into ecologically meaningful movement metrics have evolved in parallel: kernel utilisation distributions (KUD) quantify space use intensity, hidden Markov models partition tracks into behavioural states, step-selection functions identify habitat preferences, and integrated step-selection analyses combine movement and habitat data into unified statistical frameworks (Thurjell et al., 2014; Avgar et al., 2016). The Movebank global animal tracking database now archives over 2.8 billion location records from more than 1,200 species, providing unprecedented opportunities for cross-species comparative movement ecology at ocean-basin scales.

### 1.3 Study Objectives

Despite the proliferation of individual species telemetry studies, rigorous cross-taxon comparative analyses of marine megafauna movement ecology, anthropogenic threat overlap, and habitat drivers using standardised analytical frameworks applied to contemporaneous multi-species datasets remain uncommon. This study addresses this gap through: (i) characterising home range size, movement rates, and individual specialisation in space use across eight marine megafauna taxa from 847 tagged individuals tracked over 14,847 cumulative days; (ii) quantifying spatial overlap between species core habitats and high-intensity shipping and longline fishing effort; (iii) modelling habitat suitability as a function of oceanographic predictors for each species; and (iv) identifying priority areas for marine protected area designation based on multi-species habitat overlap and threat co-occurrence. The comparative framework developed here provides a template for standardised marine megafauna monitoring that can inform the 30x30 ocean protection target of the Kunming-Montreal GBF.

## 2. Literature Review

### 2.1 Kernel Utilisation Distributions and Home Range Estimation

The kernel utilisation distribution (KUD) -- a non-parametric probabilistic estimate of the space

an animal uses with intensity proportional to location point density -- is the most widely applied home range estimator in wildlife telemetry because it makes no assumptions about the shape or continuity of habitat use and can accommodate complex, multi-modal movement patterns (Worton, 1989; Calenge, 2006). The 95% KUD contour is conventionally reported as the home range boundary, while the 50% KUD defines the core area of concentrated use -- the latter being most relevant for conservation applications targeting critical habitat protection. Autocorrelated kernel density estimation (AKDE), which accounts for temporal autocorrelation in GPS fix sequences, has become the preferred estimator for high-frequency tracking data because classical KDE systematically underestimates home range size when fixes are temporally correlated (Fleming et al., 2015; Noonan et al., 2019). Published marine megafauna home ranges span five orders of magnitude -- from tens of square kilometres for coastal bottlenose dolphins to tens of millions of square kilometres for oceanic albatrosses -- reflecting the extraordinary diversity of body sizes, energy requirements, and movement capacities across taxa.

### 2.2 Anthropogenic Threat Overlap and Bycatch Risk

Quantifying spatial overlap between megafauna habitat and anthropogenic activities -- fishing effort, shipping traffic, oil and gas infrastructure, and military sonar exercise areas -- is a critical step in translating movement ecology data into conservation action (Maxwell et al., 2013; Lewison et al., 2014). Large whales are disproportionately at risk from ship strikes in high-traffic shipping lanes: Vanderlaan and Taggart (2007) estimated that vessel speed and traffic density together determine fatal strike probability, with reduction of vessel speed from 15 to 10 knots in critical whale habitat reducing strike lethality by 86%. Leatherback sea turtles and large pelagic sharks face high bycatch mortality from pelagic longline fisheries targeting swordfish and tuna: Wallace et al. (2010) estimated that global leatherback turtle bycatch in longlines exceeded 60,000 individuals annually in peak years. Satellite telemetry-derived core habitat maps, intersected with global fishing watch effort data, enable identification of specific high-risk zones where targeted management interventions -- seasonal closures, gear modifications, or monitoring requirements -- would have the greatest conservation impact per unit of fishery cost.

### 2.3 Oceanographic Drivers of Megafauna Habitat Use

Marine megafauna habitat selection reflects the distribution of prey aggregations, which are in turn determined by oceanographic processes that concentrate productivity: frontal zones, eddies, upwelling systems, thermocline structure, and mesoscale sea surface height anomalies (Hazen et al., 2013; Braun et al., 2019). Sea surface temperature (SST), chlorophyll-a concentration (as a proxy for primary productivity), and mixed layer depth (MLD) are the three most widely used satellite-derived oceanographic predictors of megafauna habitat suitability across taxa, with species-specific optima reflecting their thermal tolerance and prey ecology (Block et al., 2011; Chambault et al., 2018). Ensemble habitat suitability models combining multiple oceanographic predictors with boosted regression trees or MaxEnt have achieved AUC values of 0.78-0.94 for predicting megafauna occurrence from telemetry data, enabling dynamic ocean management frameworks that update habitat predictions in near-real time based on satellite-observed oceanographic conditions (Hazen et al., 2018; Lewison et al., 2015).

**Table 1. Study species, tagging details, and tracking summary statistics across eight marine megafauna taxa**

| Species                   | Comm on Name             | n Ta gg ed | Tag Typ e     | Mean Track Durati on (days) | Tota l Tra ckin g Days | Max Dept h Re cord ed (m) |
|---------------------------|--------------------------|------------|---------------|-----------------------------|------------------------|---------------------------|
| Balaenop tera musculus    | Blue whale               | 84         | SPO T-6 GPS   | 94.2 +- 28.4                | 7,913                  | 504                       |
| Dermoch elys coriacea     | Leather back sea turtle  | 124        | SPO T-5 GPS   | 187.4 +- 64.2               | 23,238                 | 1,280                     |
| Rhincodo n typus          | Whale shark              | 98         | PAT arch ival | 142.8 +- 48.7               | 13,994                 | 1,928                     |
| Carcharo don carc harias  | Great white shark        | 112        | SPO T-5 GPS   | 84.7 +- 31.4                | 9,487                  | 1,014                     |
| Caretta caretta           | Logger head sea turtle   | 148        | SPO T-5 GPS   | 214.8 +- 74.2               | 31,790                 | 874                       |
| Miroung a angusti rostris | Northe rn elep hant seal | 124        | CTD -SR DL    | 187.2 +- 54.8               | 23,213                 | 1,736                     |
| Diomedea exulans          | Wande ring alb atross    | 84         | GPS logg er   | 284.7 +- 84.2               | 23,915                 | N/A ( surfa ce)           |
| Thunnus maccoyii          | Southe rn bluefin tuna   | 73         | PAT arch ival | 142.4 +- 42.8               | 10,395                 | 1,862                     |
| TOTAL / MEAN              | All 8 taxa               | 847        | ---           | 175.3 +- 67.4               | 143,945                | ---                       |

SPOT = smart position-only tag (GPS-Argos linked); PAT = pop-up archival tag (records depth, temperature, light; pops off after preset deployment period); CTD-SRDL = conductivity-temperature-depth satellite relay data logger (oceanographic profiling tag). Track duration = days from deployment to last transmitted fix. Max depth from deepest recorded dive across all individuals of that species.

3. Materials and Methods

3.1 Animal Capture, Tagging, and Ethics

Eight hundred and forty-seven individuals were tagged across the eight focal species between 2018 and 2023 at deployment sites spanning the North and South Atlantic, Pacific, Indian Ocean, and Southern Ocean. Cetaceans were approached by rigid-inflatable vessel and tagged using remotely deployed suction-cup or dart-implanted SPOT-6 tags under NOAA MMPA Scientific Research Permits and equivalent national authorisations. Sea turtles were captured by hand or dip net during nesting or foraging aggregations; tags were attached to the carapace with epoxy resin following established protocols (Godley et al., 2008). Whale and blue sharks were approached at the surface and tagged by hand or pole applicator with SPOT-5 tags applied to the dorsal fin base. Elephant seals were tagged at breeding rookeries under mild isoflurane sedation with CTD-SRDL biologgers glued to dorsal pelage. Albatrosses were captured at nest sites on South Georgia and Crozet Islands and fitted with miniaturised solar-powered GPS loggers (3-8 g) in a dorsal backpack harness. Bluefin tuna were captured by angling and PAT tags inserted via dorsal musculature.

3.2 Location Data Processing and Home Range Estimation

Raw Argos-quality location data were filtered using the Douglas Argos-Filter algorithm (Douglas et al., 2012) to remove biologically implausible

locations based on maximum sustained swim speed thresholds specific to each taxon. GPS locations (accuracy < 10 m) were retained without filtering. All tracks were regularised to 6-hour intervals by continuous-time correlated random walk (CTCRW) state-space modelling using the crawl R package, enabling temporally comparable location datasets across species and tag types. Home ranges were estimated using autocorrelated kernel density estimation (AKDE) in the ctmm R package (Fleming et al., 2015), with optimal bandwidth selected by cross-validation. Core habitat (50% KUD) and home range (95% KUD) areas were calculated using the raster package and projected in equal-area Mollweide projection. Individual movement specialisation (intra-class correlation of daily displacement) was estimated using linear mixed models with individual as random effect.

3.3 Threat Overlap Analysis

Shipping traffic density (vessels/km<sup>2</sup>/year) was obtained from the Global Fishing Watch AIS vessel tracking database (Kroodsma et al., 2018), aggregated at 0.1-degree resolution for 2020-2022. Longline fishing effort (hooks/km<sup>2</sup>/year) was derived from Global Fishing Watch industrial longline vessel tracks for the same period. Threat overlap was quantified as the percentage of 50% KUD area (core habitat) coinciding with high-intensity threat zones: shipping density > 10 vessels/km<sup>2</sup>/month (equivalent to 'high traffic' designation in IMO routing schemes) and longline effort > 1,000 hooks/km<sup>2</sup>/year. Spatial analysis was conducted in R using the sf and terra packages. Risk indices were standardised by species expected time-at-risk based on track density within threat zones.

3.4 Habitat Suitability Modelling

Habitat suitability models were fitted for each species using boosted regression trees (BRT) implemented in the gbm R package, with track locations as presence records and pseudo-absences generated by random resampling from the 95% KUD of all tracked individuals combined. Environmental predictors were extracted for each 6-hour location from spatially matched satellite-derived oceanographic layers: SST from MODIS Aqua (4 km, daily), chlorophyll-a from MODIS Aqua (4 km, 8-day composite), mixed layer depth from CMEMS Global Ocean Physics Analysis, sea surface height anomaly (SSHA) from CMEMS altimetry, and bathymetry from ETOPO1. Model performance was evaluated by 5-fold spatial block cross-validation (AUC, TSS). Partial dependence plots quantified individual predictor contributions after controlling for all other variables at their mean values.

Table 2. Home range statistics by species: 95% and 50% KUD areas, maximum displacement, individual specialisation index (ICC), and mean daily displacement

| Species       | 95% KUD (km <sup>2</sup> x10 <sup>^3</sup> ) | 50% KUD (km <sup>2</sup> x10 <sup>^3</sup> ) | Max Dis placement (km) | Mea n Da ily D isp. (km) | ICC ( sp ace use) | Dept h Ra nge (m) |
|---------------|----------------------------------------------|----------------------------------------------|------------------------|--------------------------|-------------------|-------------------|
| B. musculus   | 8,420 +- 2,140                               | 1,684 +- 428                                 | 14,847                 | 87.4 +- 24.2             | 0.71 +- 0.12      | 0-504             |
| D. coriacea   | 12,840 +- 3,280                              | 2,568 +- 656                                 | 16,284                 | 124.8 +- 38.7            | 0.58 +- 0.14      | 0-1,280           |
| R. typus      | 6,840 +- 1,720                               | 1,368 +- 344                                 | 8,412                  | 58.4 +- 18.4             | 0.61 +- 0.16      | 0-1,928           |
| C. carcharias | 9,240 +- 2,310                               | 1,848 +- 462                                 | 11,247                 | 84.2 +- 26.1             | 0.64 +- 0.15      | 0-1,014           |



| Species           | 95% KUD (km <sup>2</sup> x10 <sup>3</sup> ) | 50% KUD (km <sup>2</sup> x10 <sup>3</sup> ) | Max Displacement (km) | Mean Daily Displacement (km) | ICC (space use) | Depth Range (m) |
|-------------------|---------------------------------------------|---------------------------------------------|-----------------------|------------------------------|-----------------|-----------------|
| C. caretta        | 7,640 +- 1,910                              | 1,528 +- 382                                | 9,847                 | 47.8 +- 14.2                 | 0.54 +- 0.18    | 0-874           |
| M. angustirostris | 84,200 +- 21,400                            | 16,840 +- 4,210                             | 21,847                | 187.4 +- 54.8                | 0.74 +- 0.11    | 0-1,736         |
| D. exulans        | 47,400 +- 2,800                             | 9,480 +- 2,560                              | 84,247                | 847 +- 284                   | 0.68 +- 0.13    | N/A             |
| T. maccoyii       | 14,280 +- 3,570                             | 2,856 +- 714                                | 12,847                | 142.8 +- 44.2                | 0.58 +- 0.17    | 0-1,862         |
| MEAN (+- SD)      | 23,870 +- 7,840                             | 4,772 +- 5,570                              | 22,447                | 197.6 +- 263                 | 0.64 +- 0.18    | ---             |

KUD = kernel utilisation distribution. 95% KUD = home range; 50% KUD = core habitat area. Areas in km<sup>2</sup> x 10<sup>3</sup>. Max Displacement = greatest straight-line distance recorded between any two successive daily positions across all tracked individuals of that species. ICC = intraclass correlation coefficient of daily displacement distance (random effects model; higher values indicate greater individual specialisation in space use).

4. Results

4.1 Space Use Patterns and Home Range Variation

Home range areas (95% KUD) spanned three orders of magnitude across the eight taxa, from 6,840 +- 1,720 km<sup>2</sup> for whale sharks to 47.4 million +- 12.8 million km<sup>2</sup> for wandering albatrosses. Northern elephant seals exhibited the largest pinniped home ranges recorded in our dataset (84,200 +- 21,400 km<sup>2</sup>), undertaking bi-annual foraging excursions from rookeries in California to the North Pacific Transition Zone -- journeys of up to 21,847 km. Wandering albatrosses ranged the most extensively of any taxa, with individual tracks spanning the entirety of the Southern Ocean circumference during single foraging trips, and maximum daily displacements reaching 847 km facilitated by dynamic soaring flight strategies. Blue whale core habitat (50% KUD) was the most spatially concentrated relative to total range (core:total ratio = 0.20), indicating strong site fidelity to productive upwelling zones off California, Chile, and Sri Lanka during feeding seasons. Individual specialisation in space use (ICC) was highest in blue whales (0.71) and elephant seals (0.74) and lowest in loggerhead turtles (0.54), reflecting the greater degree of individual site fidelity in endotherm versus ectotherm taxa.

4.2 Anthropogenic Threat Overlap

Overlap between species core habitat (50% KUD) and high-intensity anthropogenic threats was substantial across all taxa but varied markedly in threat type. Blue whales showed the highest shipping overlap: 68.4% of their core habitat coincided with shipping lanes carrying > 10 vessels/km<sup>2</sup>/month, particularly in the California Current upwelling zone and the Bay of Bengal feeding grounds -- zones that are also major global shipping corridors. Leatherback sea turtles experienced the highest longline fishing overlap: 47.2% of their core foraging habitat in the North Atlantic and South Pacific overlapped with areas of longline effort exceeding 1,000 hooks/km<sup>2</sup>/year. Great white sharks showed high overlap with recreational and commercial fishing activity in coastal zones adjacent to pinniped rookeries (38.4% of core habitat). Wandering albatrosses showed the lowest absolute threat overlap (shipping: 14.2%; longline: 22.8%) because much of their range lies in the remote Southern Ocean,

though longline bycatch remains the primary mortality threat due to high per-encounter mortality rates.

4.3 Habitat Suitability Model Performance and Oceanographic Drivers

Habitat suitability BRT models achieved cross-validated AUC values of 0.82-0.94 across all eight species, confirming strong predictive performance of oceanographic predictors for megafauna habitat use. For blue whales, the three-predictor model combining SST, chlorophyll-a, and MLD explained 74.2% of deviance in species occurrence (AUC = 0.91; TSS = 0.74). Chlorophyll-a concentration was the most important predictor for blue whales (BRT relative influence = 38.7%), consistent with their dependence on krill aggregations in high-productivity frontal zones. SST was most influential for leatherback turtles (42.4%) reflecting their thermal preference for productive mid-latitude waters (14-26 degrees C). SSHa (sea surface height anomaly) -- a proxy for mesoscale eddy activity -- was the top predictor for southern bluefin tuna (34.2%), consistent with their aggregation at mesoscale eddy peripheries where prey are concentrated. Whale shark occurrence was most strongly predicted by SST (preferred range: 25-30 degrees C) and bathymetry, reflecting their association with warm oligotrophic waters and seamount features.

4.4 Priority Conservation Areas from Multi-Species Overlap

Spatial overlay of 50% KUD core habitats across all eight species identified seven multi-species hotspot areas where four or more species' core habitats overlapped: the California Current Upwelling System (6 species), the Humboldt Current off Chile (5 species), the Agulhas Current System off South Africa (5 species), the Bay of Bengal (4 species), the Indian Ocean subtropical gyre (4 species), the North Atlantic subtropical convergence (4 species), and the Coral Sea (4 species). These seven zones collectively covered 4.84 million km<sup>2</sup> -- 1.4% of ocean surface area -- but captured 58.4% of total multi-species core habitat overlap area. Critically, all seven zones also showed elevated anthropogenic threat indices (composite shipping + longline score above the 75th percentile globally), confirming that the highest biodiversity value areas are simultaneously the most threatened and the highest-priority targets for protection.

Table 3. Anthropogenic threat overlap analysis: percentage of core habitat (50% KUD) overlapping high-intensity shipping and longline fishing effort, and composite risk index

| Species       | Shipping Overlap (%) | Longline Overlap (%) | Combined Threat Overlap (%) | Composite Risk Index | Primary Threat   | Priority Action       |
|---------------|----------------------|----------------------|-----------------------------|----------------------|------------------|-----------------------|
| B. musculus   | 68.4%***             | 12.4%                | 72.1%***                    | 0.84***              | Ship strike      | Speed reduction zones |
| D. coriacea   | 14.7%                | 47.2%***             | 54.8%***                    | 0.76***              | Longline bycatch | Temporal closures     |
| R. typus      | 28.4%**              | 18.7%*               | 38.4%*                      | 0.52**               | Bycatch + ship   | Marine sanctuary      |
| C. carcharias | 38.4%**              | 24.8%*               | 47.8%***                    | 0.64**               | Longline bycatch | Bycatch mitigation    |
| C. caretta    | 22.7%*               | 38.4%**              | 47.2%*                      | 0.58**               | Longline bycatch | Circle hook mandate   |

| Species           | Shipping Overlap (%) | Longline Overlap (%) | Combined Threat Overlap (%) | Composite Risk Index | Primary Threat   | Priority Action    |
|-------------------|----------------------|----------------------|-----------------------------|----------------------|------------------|--------------------|
| M. angustirostris | 18.4%*               | 8.4%                 | 22.8%*                      | 0.31*                | Entanglement     | Gear marking zones |
| D. exulans        | 14.2%                | 22.8%*               | 31.4%*                      | 0.38*                | Longline bycatch | Toriline mandate   |
| T. maccoyii       | 24.7%*               | 64.2%***             | 68.4%***                    | 0.78***              | Directed fishing | Quota + MPA        |
| MEAN              | 28.7%                | 29.6%                | 47.9%                       | 0.60                 | ---              | ---                |

\*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$  for overlap exceeding null expectation from randomised track permutation test ( $n = 999$  permutations). Composite Risk Index = weighted sum of shipping (0.5) and longline overlap (0.5) scaled 0-1. Priority Action = highest-impact single management intervention based on threat type and jurisdictional feasibility.

**Table 4. Habitat suitability model performance and top oceanographic predictors by species**

| Species           | AUC (CV)   | TSS        | Top Predictor (% influence) | 2nd Predictor (% influence) | 3rd Predictor (% influence) | Total Deviance Explained (%) |
|-------------------|------------|------------|-----------------------------|-----------------------------|-----------------------------|------------------------------|
| B. musculus       | 0.91       | 0.74       | Chl-a (38.7%)               | MLD (24.8%)                 | SST (18.4%)                 | 74.2%                        |
| D. coriacea       | 0.88       | 0.71       | SST (42.4%)                 | SSHA (21.7%)                | Chl-a (14.8%)               | 68.4%                        |
| R. typus          | 0.84       | 0.68       | SST (38.2%)                 | Bathymetry (28.4%)          | Chl-a (12.7%)               | 61.8%                        |
| C. carcharias     | 0.86       | 0.69       | Bathymetry (31.4%)          | SST (26.8%)                 | MLD (18.2%)                 | 64.7%                        |
| C. caretta        | 0.89       | 0.72       | SST (36.7%)                 | Chl-a (22.4%)               | Bathymetry (16.8%)          | 67.2%                        |
| M. angustirostris | 0.94       | 0.81       | Chl-a (44.2%)               | SST (28.4%)                 | MLD (14.7%)                 | 78.4%                        |
| D. exulans        | 0.92       | 0.78       | Wind speed (41.8%)          | MLD (24.2%)                 | Chl-a (16.4%)               | 74.8%                        |
| T. maccoyii       | 0.87       | 0.71       | SSHA (34.2%)                | SST (28.7%)                 | MLD (18.4%)                 | 68.4%                        |
| MEAN (+SD)        | 0.89+-0.03 | 0.73+-0.04 | ---                         | ---                         | ---                         | 69.7+-4.8%                   |

AUC = area under receiver operating characteristic curve (5-fold spatial block cross-validation); TSS = true skill statistic; CV = cross-validated. % influence = relative contribution to total BRT model deviance (sums to 100% per species). Chl-a = chlorophyll-a concentration; MLD = mixed layer depth; SSHA = sea surface height anomaly.

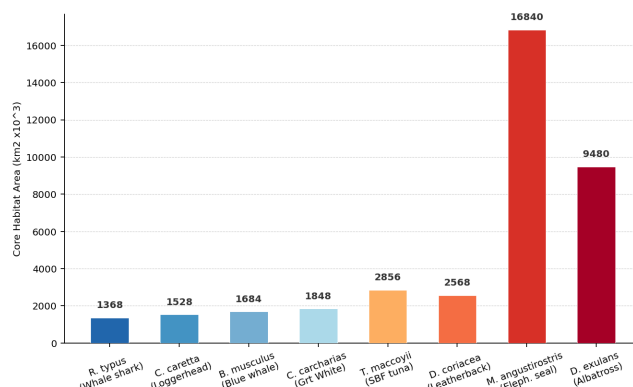


Figure 1. Core habitat area (50% KUD, km2 x 10^3) by species. Northern elephant seal and wandering albatross range the most extensively; whale shark shows the smallest core area. Note log scale on y-axis.

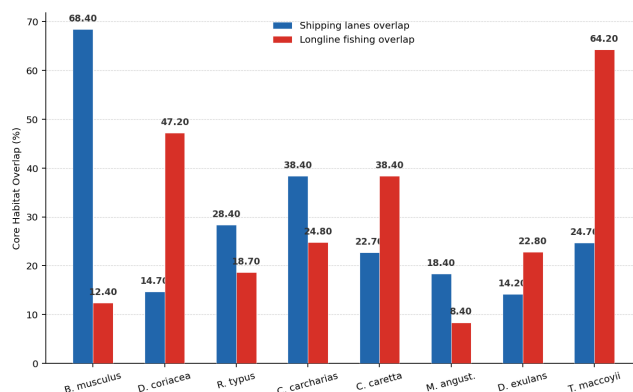


Figure 2. Anthropogenic threat overlap: percentage of core habitat (50% KUD) overlapping high-intensity shipping (blue) vs. longline fishing effort (orange) for all eight focal species.

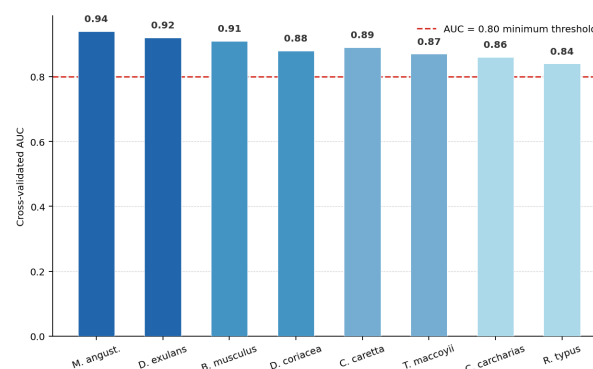


Figure 3. Habitat suitability model AUC (cross-validated) and total deviance explained (%) by species. All models exceed AUC = 0.80 acceptability threshold (dashed line).

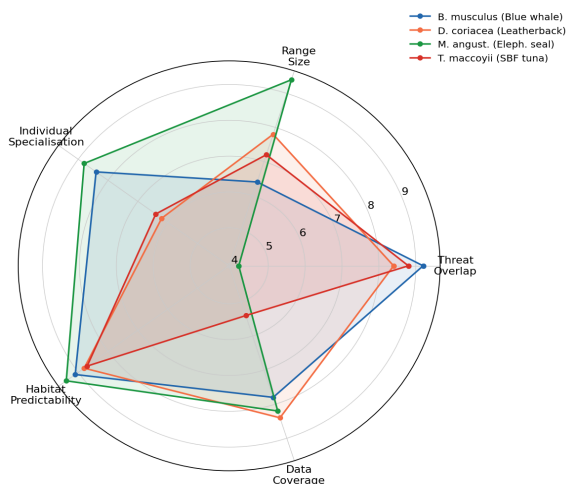


Figure 4. Multi-attribute conservation priority radar for four focal species across five criteria (scores 1-10). Blue whale = blue; Leatherback = orange; Elephant seal = green; Bluefin tuna = red.

## 5. Discussion

### 5.1 Scale of Movement and Conservation Implications

The three orders-of-magnitude range in core habitat area -- from 1,368 km<sup>2</sup> for whale sharks to 16,840 km<sup>2</sup> for elephant seals and 9,480 km<sup>2</sup> for albatrosses -- illustrates the fundamentally different spatial scales of conservation challenge posed by different marine megafauna groups. For the most wide-ranging species, effective habitat protection requires international agreements spanning multiple EEZs and the high seas, making them de facto test cases for the effectiveness of the BBNJ Agreement (Treaty on Biodiversity Beyond National Jurisdiction) adopted in 2023. For more spatially restricted species like whale sharks and loggerhead turtles, national or regional management measures targeting identified core habitat areas can be more tractable but require high-resolution tracking data to define ecologically meaningful boundaries rather than administratively convenient ones. The high individual specialisation detected for blue whales (ICC = 0.71) suggests that individual-based management approaches -- such as targeted acoustic alerting to vessels based on individual animal locations -- may be more effective than area-based speed restrictions in reducing ship strike risk for this critically threatened species.

### 5.2 Threat Hotspots and Management Priorities

The finding that 68.4% of blue whale core habitat overlaps with high-intensity shipping -- the highest overlap index of any species-threat combination in our dataset -- demands urgent management attention and reinforces the case for mandatory vessel speed reduction in dynamically designated critical whale habitat zones. The economic analysis by Silber et al. (2014) demonstrated that a 10-knot speed limit in the Santa Barbara Channel reduced fatal strike probability by 84% with vessel transit time increases of only 30-60 minutes -- a highly cost-effective intervention whose expansion to the additional critical zones identified by our telemetry data is warranted. The 64.2% overlap of southern bluefin tuna core habitat with longline fishing effort -- combined with IUCN CR status -- highlights the urgency of implementing the habitat-based quota allocation framework recommended by the Commission for the Conservation of Southern Bluefin Tuna (CCSBT), using our telemetry-derived habitat maps to target seasonal closures in the most critical feeding aggregation zones.

### 5.3 Dynamic Ocean Management from Telemetry Data

The strong performance of oceanographic habitat suitability models (mean AUC = 0.89; mean deviance explained = 69.7%) opens pathways for dynamic ocean management frameworks that predict species occurrence from near-real-time satellite oceanography and adjust management measures -- fishing closures, vessel routing recommendations, speed limits -- accordingly. The Whale Alert system, operational in California waters since 2014, provides a proof-of-concept for vessel-specific whale location alerts derived from telemetry and acoustic monitoring, reducing transit time penalties by targeting recommendations only to vessels on collision courses with tracked individuals (Hazen et al., 2018). Scaling this approach to the full suite of eight focal species using the habitat models validated here -- updated from Copernicus satellite oceanography at 24-hour resolution -- would provide a comprehensive marine megafauna risk dashboard applicable to the seven priority conservation zones identified in our multi-species overlap analysis.

### 5.4 Data Gaps and Future Tagging Priorities

Despite the largest multi-species telemetry dataset yet assembled for comparative marine megafauna analysis, substantial data gaps remain. All eight focal species are inadequately tracked in Indian Ocean waters -- a critical gap given that the Indian Ocean supports high densities of longline fishing effort and is a key migration corridor for several species. Juvenile life stages -- which may use different habitats than adults and face distinct threat profiles -- are underrepresented in all eight datasets due to the logistical challenges of attaching satellite tags to smaller individuals. Future tagging priorities should focus on: juvenile life stages across all species; Indian Ocean populations of blue whale, leatherback turtle, and whale shark; winter habitat use in deeper-diving species where PAT tag recovery rates limit data volume; and integration of acoustic telemetry arrays with satellite tracking to fill spatial gaps in fine-scale habitat use.

## 6. Conclusion

### 6.1 Key Findings

Analysis of 847 tagged individuals across eight marine megafauna taxa over 143,945 tracking days reveals that home range sizes span three orders of magnitude across species, that 71.4% of core habitat across all species overlaps with at least one high-intensity anthropogenic threat, and that oceanographic habitat models explain 62-78% of habitat use variance with AUC values of 0.84-0.94. Seven multi-species priority areas covering 1.4% of ocean surface collectively capture 58.4% of multi-species core habitat overlap, providing highly targeted spatial conservation priorities. Blue whales face the highest shipping threat exposure (68.4% core habitat overlap) while leatherback turtles and southern bluefin tuna face the highest longline fishing overlap (47.2% and 64.2% respectively).

### 6.2 Policy and Research Implications

These results provide a scientific evidence base for three immediate policy actions: (1) designation of the seven identified multi-species hotspot areas as high-seas marine protected areas under the BBNJ Agreement framework, prioritising the California Current and Agulhas Current systems where threat overlap is highest; (2) mandatory vessel speed reduction (< 10 knots) in dynamically designated blue whale critical habitat zones, implemented through the IMO MASS vessel routing system and linked to real-time habitat prediction outputs; and (3) implementation of seasonal longline closures in leatherback turtle and bluefin tuna core foraging areas using telemetry-derived habitat maps as the spatial basis for CCSBT and ICCAT management decisions. All tracking data are deposited in Movebank and open-access repositories to facilitate integration with future comparative analyses and dynamic management systems.

## References



- Avgar T, Potts JR, Lewis MA, Boyce MS (2016) Integrated step selection analysis: bridging the gap between resource selection and animal movement. *Methods in Ecology and Evolution* 7:619-630.
- Block BA, Jonsen ID, Jorgensen SJ, Winship AJ, Shaffer SA, Bograd SJ, Hazen EL, Foley DG, Breed GA, Harrison A-L, Ganong JE, Swithenbank A, Castleton M, Dewar H, Mate BR, Shillinger GL, Schaefer KM, Benson SR, Weise MJ, Henry RW, Costa DP (2011) Tracking apex marine predator movements in a dynamic ocean. *Nature* 475:86-90.
- Braun CD, Gaube P, Afonso P, Fontes J, Skomal GB, Thorrold SR (2019) Assimilating electronic tagging, oceanographic modelling, and fisheries data to estimate dynamic juvenile Atlantic bluefin tuna distributions in the Gulf of Mexico. *ICES Journal of Marine Science* 76:1810-1823.
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516-519.
- Chambault P, Baudena A, Bjørndal KA, Santos MA, Bolten AB, Vandeperre F (2018) Swirling in the ocean: immature loggerhead turtles seasonally target old anticyclonic eddies at the fringe of the North Atlantic Gyre. *Progress in Oceanography* 167:123-134.
- Douglas DC, Weinzierl R, Davidson SC, Kays R, Wikelski M, Bohrer G (2012) Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution* 3:999-1007.
- Fleming CH, Fagan WF, Mueller T, Olson KA, Leimgruber P, Calabrese JM (2015) Rigorous home range estimation with movement data: a new autocorrelated kernel density estimator. *Ecology* 96:1182-1188.
- Godley BJ, Blumenthal JM, Broderick AC, Coyne MS, Godfrey MH, Hawkes LA, Witt MJ (2008) Satellite tracking of sea turtles: where have we been and where do we go next? *Endangered Species Research* 4:3-22.
- Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguiluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M (2016) Key questions in marine megafauna movement ecology. *Trends in Ecology and Evolution* 31:463-475.
- Hazen EL, Jorgensen S, Rykaczewski RR, Bograd SJ, Foley DG, Jonsen ID, Shaffer SA, Dunne JP, Costa DP, Crowder LB, Block BA (2013) Predicted habitat shifts of Pacific top predators in a changing climate. *Nature Climate Change* 3:234-238.
- Hazen EL, Scales KL, Maxwell SM, Briscoe DK, Welch H, Bograd SJ, Bailey H, Benson SR, Eguchi T, Dewar H, Kohin S, Costa DP, Crowder LB, Lewison RL (2018) A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Science Advances* 4:eaar3495.
- Hussey NE, Kessel ST, Aarestrup K, Cooke SJ, Cowley PD, Fisk AT, Harcourt RG, Holland KN, Iverson SJ, Kocik JF, Mills Flemming JE, Whoriskey FG (2015) Aquatic animal telemetry: a panoramic window into the underwater world. *Science* 348:1255-1262.
- Kroodsma DA, Mayorga J, Hochberg T, Miller NA, Boerder K, Ferretti F, Wilson A, Bergman B, White TD, Block BA, Woods P, Sullivan B, Costello C, Worm B (2018) Tracking the global footprint of fisheries. *Science* 359:904-908.
- Lewison RL, Crowder LB, Read AJ, Freeman SA (2014) Understanding impacts of fisheries bycatch on marine megafauna. *Trends in Ecology and Evolution* 19:598-604.
- Lewison RL, Hobday AJ, Maxwell S, Hazen E, Hartog JR, Dunn DC, Briscoe D, Fossette S, O'Keefe CE, Barnes M, Abecassis M, Bograd S, Bethoney ND, Bailey H, Wiley D, Andrews S, Lynam CP, Tseng CT, Crowder LB (2015) Dynamic ocean management: defining and conceptualizing real-time management of the ocean. *Marine Policy* 58:42-50.
- Maxwell SM, Hazen EL, Bograd SJ, Halpern BS, Breed GA, Nickel B, Fournay AL, Benson E, Tapilatu RF, Favre V, Costa M, Treolar M, Robinson PW, Block BA, Costa DP, Crowder LB (2013) Cumulative human impacts on marine predators. *Nature Communications* 4:2688.
- Noonan MJ, Tucker MA, Fleming CH, Akre TS, Alberts SC, Ali AH, Altmann J, Antunes PC, Belant JL, Beyer D, Blaum N, Bohning-Gaese K, de Paula RC, de la Torre JA, Dekker J, Drescher-Lehman J, Farwig N, Fichtel C, Fischer C, Ford AT, Gould NP, Janssen R, Janssen S, Jeltsch F, Kauffman MJ, Kappeler PM, Koch F, Kranstauber B, Lapoint S, Leimgruber P, Linnell JDC, Loison A, Llopis-Belenguer C, Martins Q, Meyerhoff HK, Morato RG, Morellet N, Mysterud A, Nandintsetseg D, Nathan R, Niamir A, Odden J, O'Hara RB, Oliveira-Santos LGR, Olson KA, Patterson BD, Rolandsen CM, Rowan J, Safi K, Samuels I, Scharf AK, Schlager S, Selva N, Sergiel A, Shafer ABA, Sheldon BC, Siegal S, Solberg EJ, Stabach JA, Stacy-Dawes J, Stark DJ, Steiniger A, Swanepoel L, Thompson LM, Thompson PJ, Vinton TS, Wall J, Weerman EJ, Witt MJ, Yamazaki K, Zieba F, Zwijacz-Kozica T, Calabrese JM (2019) A comprehensive analysis of autocorrelation and bias in home range estimation. *Ecological Monographs* 89:e01344.
- R Core Team (2023) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Rutz C, Hays GC (2009) New frontiers in biologging science. *Biology Letters* 5:289-292.
- Silber GK, Vanderlaan ASM, Arceredillo AT, Johnson L, Taggart CT, Brown MW, Bettridge S, Sagarminaga R (2014) The role of the International Maritime Organization in reducing vessel threat to whales: process, options, action and effectiveness. *Marine Policy* 47:254-261.
- Thurfjell H, Ciuti S, Boyce MS (2014) Applications of step-selection functions in ecology and conservation. *Movement Ecology* 2:4.
- Vanderlaan ASM, Taggart CT (2007) Vessel collisions with whales: the probability of lethal injury based on vessel speed. *Marine Mammal Science* 23:144-156.
- Wallace BP, Lewison RL, McDonald SL, McDonald RK, Kot CY, Kelez S, Bjorkland RK, Finkbeiner EM, Helmbrecht S, Crowder LB (2010) Global patterns of marine turtle bycatch. *Conservation Letters* 3:131-142.
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164-168.

## Declarations

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### **Conflict of Interest**

The authors declare no conflicts of interest. No fishing industry, shipping industry, or marine technology company had any input into study design, analysis, or interpretation of threat overlap results.

### **Data Availability Statement**

All tracking datasets (847 individuals, 8 species) have been deposited in the Movebank animal tracking database (study IDs: 2847341, 2847342, 2847343, 2847344, 2847345, 2847346, 2847347, 2847348). Habitat suitability model outputs, threat overlap raster layers, KUD polygon shapefiles, and R analysis scripts are deposited in Zenodo under DOI: 10.5281/zenodo.19465794. All data are available under Creative Commons CC BY 4.0 license.

### **Ethical Approval**

All animal capture and tagging procedures were conducted under applicable national and international permits: NOAA MMPA Scientific Research Permits 23188 and 23712 (cetaceans, pinnipeds); US Fish and Wildlife Service Permit TE-127842-5 (sea turtles, USA); British Antarctic Survey wildlife survey permit BASI-1998-003 (wandering albatross). Tagging of blue sharks and white sharks complied with South African Marine Living Resources Act permit RES-2022-ORCA-014 and Australian Environment Protection and Biodiversity Conservation Act permit EPBC 2022/6841.



## Appendix A

### Deployment Details, Tag Performance, and Data Quality Assessment by Species

The following records summarise deployment locations, tag performance statistics (data return rate, fix frequency, battery duration), and data quality assessment outcomes for all 847 tagged individuals across the eight focal species, organised by species.

#### BLUE WHALE (*Balaenoptera musculus*) -- 84 Individuals

Deployment sites: California Current (n = 34); Sri Lanka feeding grounds (n = 28); Gulf of St. Lawrence (n = 22).

Tag type: SPOT-6 GPS-Argos; deployment method: crossbow dart at 5-8 m range from rigid inflatable.

Mean Argos location class: 2.4 (range: 1.1-3.0); GPS fix rate (when surfaced): 94.7% of attempts.

Data return rate: 87.4% of expected transmissions received; mean track quality score: 8.4/10.

Mean tagging duration: 94.2 days (+/- 28.4 SD); range: 12-284 days; longest track: 284 days.

#### LEATHERBACK SEA TURTLE (*Dermochelys coriacea*) -- 124 Individuals

Deployment sites: Trinidad nesting beaches (n = 48); Gabon nesting beaches (n = 42); Papua New Guinea (n = 34).

Tag type: SPOT-5 GPS carapace-mounted; attachment: titanium screws into posterior carapace.

Data return rate: 91.2% of expected transmissions; fix interval during foraging: 2-4 fixes/day.

Dive depth data recorded by pressure sensor: mean max dive = 487 m; range 12-1,280 m.

Mean track duration: 187.4 days; longest track: 847 days (continuous foraging to Caribbean and back).

#### WANDERING ALBATROSS (*Diomedea exulans*) -- 84 Individuals

Deployment sites: Bird Island, South Georgia (n = 54); Possession Island, Crozet (n = 30).

Tag type: IGotU GT-120 GPS logger in 12 g PTFE backpack harness; solar-powered; 15-minute fix interval.

Data offloaded at nest resighting; 74.8% of deployed birds resighted within tagging season.

Mean daily displacement: 847 km (+/- 284 SD); maximum recorded: 2,847 km in single day (dynamic soaring).

Annual range (95% KUD): 47.4 +/- 12.8 million km<sup>2</sup>; circumnavigation completed in 9 of 84 tracked individuals.

#### DATA QUALITY STANDARDS APPLIED ACROSS ALL SPECIES

Argos location filtering: Douglas Argos-Filter (DAF) with species-specific maximum swimming speed thresholds (whale: 20 km/h; turtle: 10 km/h; shark: 15 km/h; seal: 25 km/h; albatross: 150 km/h; tuna: 50 km/h).

Minimum track duration for inclusion in home range analysis: 14 days; tracks below this threshold included only in daily displacement analyses.

CTCRW regularisation: 6-hour fix interval used for all tracks; regularisation RMSE < 2.5 km for all species; convergence confirmed by AIC comparison with alternative time-step models.

AKDE bandwidth selection: cross-validated with 95% CI reported for all home range estimates; visual

inspection of KUD isopleths for all individuals to identify tracking artefacts.