Scaling of Activity Space in Marine Organisms across Latitudinal Gradients

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ABSTRACT: Unifying models have shown that the amount of space used by animals (e.g., activity space, home range) scales allometrically with body mass for terrestrial taxa; however, such relationships are far less clear for marine species. We compiled movement data from 1,596 individuals across 79 taxa collected using a continental passive acoustic telemetry network of acoustic receivers to assess allometric scaling of activity space. We found that ectothermic marine taxa do exhibit allometric scaling for activity space, with an overall scaling exponent of 0.64. However, body mass alone explained only 35% of the variation, with the remaining variation best explained by trophic position for teleosts and latitude for sharks, rays, and marine reptiles. Taxon-specific allometric relationships highlighted weaker scaling exponents among teleost fish species (0.07) than sharks (0.96), rays (0.55), and marine reptiles (0.57). The allometric scaling relationship and scaling exponents for the marine taxonomic groups examined were lower than those reported from studies that had collated both marine and terrestrial species data derived using various tracking methods. We propose that these disparities arise because previous work integrated summarized data across many studies that used differing methods for collecting and quantifying activity space, introducing considerable uncertainty into slope estimates. Our findings highlight the benefit of using large-scale, coordinated animal biotelemetry networks to address cross-taxa evolutionary and ecological questions.

Keywords: acoustic telemetry, Brownian bridge kernel utilization distribution (KUD), continental network, Integrated Marine Observing System (IMOS), metabolic theory, spatial ecology.

Introduction

An animal's activity space generally reflects essential activities, such as seeking food, shelter, reproduction, and suitable habitats as well as avoiding potential predators or unfavorable conditions (Burt 1943). Identifying the factors that contribute to an animal's activity space is important for predicting population health under a changing climate and developing effective management or conservation strategies for ecological communities under threat (Hirt et al. 2021). Within guilds of animals, activity space (i.e., space use) generally varies as a function of body weight (Turner et al. 1969; Hendriks 2007) because larger animals tend to move over larger spatial extents than smaller animals because of their greater energy requirements (McNab 1963; Lindstedt et al. 1986) and the relatively lower energetic cost of movement (Schmidt-Nielsen 1972). Allometry of activity space across animal guilds is also influenced by a range of other factors, such as locomotive strategy, trophic level, social conditions, habitat dimensionality, and prey size (Harestad and Bunnel 1979; Carbone et al. 2004; Jetz et al. 2004; Tamburello et al. 2015; Rosten et al. 2016; Sequeira et al. 2018; Boratyński et al. 2020; Todd and Nowakowski 2021).

The relative influence of intrinsic and extrinsic factors on patterns of activity space among taxa has been long debated in the scientific literature. In his seminal article, McNab (1963) proposed that the allometric body mass exponent for determining activity space size is similar to that for metabolism, 0.75. However, more recent studies have revealed much more complex relationships. For example, the scaling exponent is greatly influenced by the habitats within which species forage, with scaling exponents increasing with foraging dimensionality (Witting 1995). Comparative studies of lake- and river-dwelling freshwater fishes have shown that while the relationship between body size and activity space produced homogenous slopes across environments, lake fish always had larger activity spaces than river fish of equal body mass (Minns 1995). Furthermore, movement patterns and activity spaces of endothermic marine animals are significantly influenced by whether they forage on or off the continental shelf, with species that occupy offshore pelagic habitats displaying more directed daily movements than their coastal counterparts (Sequeira et al. 2018). Species that feed at higher trophic levels need to forage over greater distances to find their relatively less abundant prey (Lindstedt et al. 1986). Even within trophic groups, the sources of diet and prey size explain a large proportion of variation in allometric scaling of activity space (Gompper and Gittleman 1991; Tamburello et al. 2015).

Most studies assessing allometric scaling of activity space have used meta-analyses and focused on terrestrial birds, mammals, and reptiles. Terrestrial vertebrate activity spaces scale allometrically with body size, with logarithmic exponents between 0.95 and 1.14 (Jetz et al. 2004; Hatton et al. 2019). By contrast, studies of freshwater fishes have reported a far lower scaling exponent of only 0.58 (Minns 1995). Allometric scaling in the marine environment was, until recently, poorly studied. Only a limited

number of studies have reported allometric scaling of activity space for marine animals (i.e., Nash et al. 2015; Tamburello et al. 2015). These studies reported that the scaling exponent for marine fishes is steeper than those of either terrestrial vertebrates or freshwater fish at 1.12 and 1.71, respectively (Nash et al. 2015; Tamburello et al. 2015). Nash et al. (2015) highlighted an important potential confounding factor: most allometric studies derived scaling coefficients using animal activity space data from multiple studies that used a range of techniques (i.e., visual tracking, mark-recapture, telemetry, mixed methods), potentially affecting scaling coefficients. They also highlighted that over time, the principal method used to define activity space shifted from minimum convex polygons up to the early 1990s to kernel utilization distributions (KUDs). This change in approach could readily add a methodological source of uncertainty, as opposed to a biological source, in describing the relationship between activity space and body size. Tamburello et al. (2015) recognized that there was likely to be significant variability among the source data and attempted to account for the method by which activity space was measured by including it as a random effect in the model. However, Tamburello et al. (2015) did not consider interstudy differences in the probability density estimator used (i.e., KUD smoothing factor). Presumably similar confounding factors also affected data collection, since data were drawn from essentially the same body of literature as that used in Nash et al. (2015). Additionally, measures of activity space and mass used to construct allometric scaling in the past have used species average values, with limited consideration of the effect of intraspecific variability in both measures (Welsh et al. 2013). Therefore, at this juncture the allometry of activity space in marine animals remains unclear.

To address these methodological issues, we compiled and assessed allometric scaling in a data set comprising 1,596 animals across 79 marine species and 34,890,047 location detections, collected over a decade and across 32 degrees of latitude. The data were collated by the Integrated Marine Observing System's (IMOS's; https://www.imos.org.au) Animal Tracking Facility. Since 2007, the IMOS Animal Tracking Facility has coordinated a continental-scale network of acoustic receiver stations that covers a significant portion of Australia's coastline (fig. 1a; Hoenner et al. 2018). This collaborative network of receivers and associated information infrastructure is used by independent researchers, universities, and government organizations to understand animal movement patterns and collect continental-scale detection data around Australia (fig. 1b). This study used a comprehensive quality-controlled data set of the movements of a range of marine taxa monitored using the IMOS Animal Tracking Facility network (Hoenner et al. 2018). Using this database, we assessed activity

space scaling laws across four major marine taxonomic groups—teleost fish, sharks, rays, and reptiles—that inhabit Australia's coastal waters, with our a priori hypothesis being that allometric scaling would be apparent and similar across these taxa. In contrast to earlier efforts (e.g., Nash et al. 2015; Tamburello et al. 2015), we examined marine ectotherms that forage in benthic and pelagic habitats and assessed activity space against body size, taxonomic group, geographic location, and trophic group. Given that activity space for all taxa was estimated at an individual level, using the same technology and analyzed using the same standardized approach (Udyawer et al. 2018), rather than summarized species-level data, this study overcomes the potential biases incurred by varying methods used to estimate activity space and incorporates intraspecific variability in measurements used to define allometric scaling relationships.

Methods

Data Collection and Processing

Metrics of activity space used to examine allometric scaling relationships for marine animals were calculated from acoustic telemetry detection data of tagged organisms collated over a decade (2007–2017) by the IMOS Animal Tracking Facility (fig. 1) and stored in an openly accessible data repository (https://animaltracking.aodn.org.au). Data available in the repository undergoes strict quality control, eliminating erroneous raw detections using specific rules that interrogate each data point in light of spatiotemporal patterns in detection and known species ranges (for the primary quality control process, see Hoenner et al. 2018). Raw detections were processed to estimate short-term centers of activity (COAs) for 60-min intervals. COAs were estimated prior to subsequent activity space estimation, to account for the varied transmission settings across tagging projects and spatial biases in raw detection data inherent in node-based telemetry studies as well as to incorporate movements of tagged animals between fixed receivers (Udyawer et al. 2018). We conducted a second round of data filtering by excluding individuals that were not detected at five unique COA locations. A minimum of five unique COA locations meant that tagged individuals recorded on a minimum of two receivers were included, provided that sufficient movements were recorded between the receivers over the tracking period. This process ensured that subsequent estimates of activity space were not biased based on lack of positional data. Detection data were used to calculate standardized metrics of activity space using the Animal Tracking Toolbox functions within the R package VTrack (Campbell et al. 2012; Udyawer et al. 2018), which allowed for direct
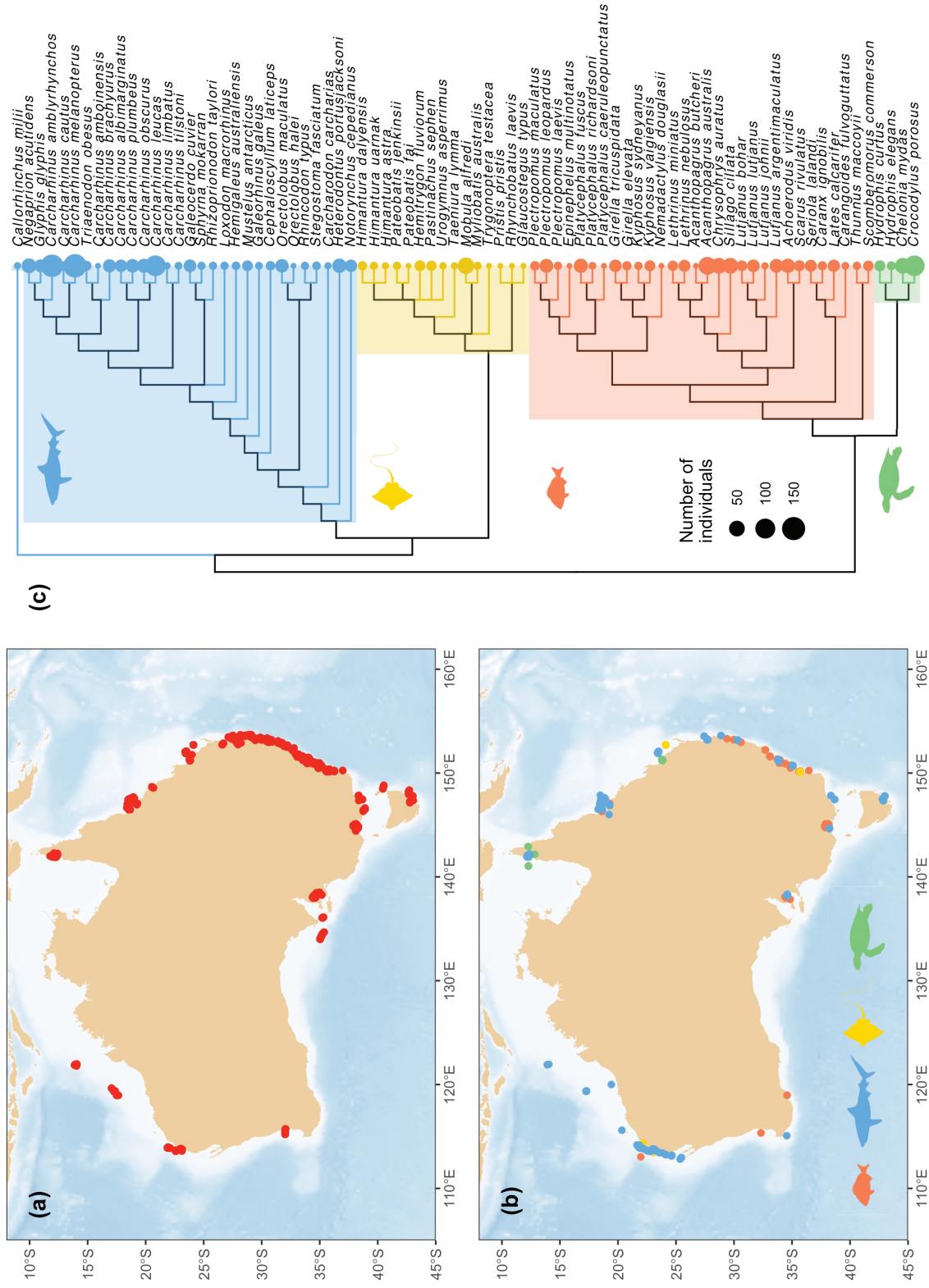
Figure 1: Map of geographic locations of acoustic receivers deployed (*a*; red points; *n* = 6,067) as part of the Integrated Marine Observing System's Animal Tracking Facility, release locations (*b*; *n* = 1,596), and number of individuals tracked from each species within four broad taxonomic groups (*c*): teleost fishes (orange), sharks (blue), rays (yellow), and marine reptiles (green). Phylogeny between groups displayed here are used for phylogenetic corrections in models.

comparison across taxa and sites. For each tagged individual, activity space included the area within the 95% contour of a utilization distribution estimated using a Brownian bridge movement model including all detections (Horne et al. 2007; fig. S1*a*). A uniform smoothing parameter associated with the listening range of acoustic telemetry methods was applied to all of the data to ensure comparability. The smoothing parameter for Brownian bridge models associated with relocation error (σ_2) was determined using an ad hoc approach (Kie 2013) and aligned with measured listening ranges of acoustic arrays within the IMOS network (e.g., Knip et al. 2012; Matley et al. 2015; Pillans et al. 2017). The smoothing parameter associated with animal speed (σ_1) was estimated using a maximum likelihood estimator following methods outlined by Calenge (2006).

We collated species identity, release location, body mass, trophic group, and foraging habitat data for each tagged individual. Each species used was classified into one of four broad taxonomic groupings: teleost fish, shark, ray, or marine reptile. Where information on body mass was not recorded, it was estimated from total length, snout-vent length, or carapace length using length-weight relationships in published literature (Webb and Messel 1978; Hirth 1982; Froese et al. 2014; Froese and Pauly 2017; fig. S1*b*). Trophic level indices for each species were sourced from published literature that used standardized indices based on diet composition (Cortés 1999; Jacobsen and Bennett 2013; Froese and Pauly 2017). Each individual was then categorized into one of three broad trophic groups: primary consumers, secondary consumers, and tertiary consumers. Foraging habitat of each species was assessed by classifying each species as either pelagic or benthic foragers (table S1).

Statistical Modeling

Metrics of individual-level activity space and body mass were used to construct a series of subset hierarchical models to identify patterns in activity space ~ mass allometry. The series of subset models used information on taxonomy, trophic grouping, foraging habitat, and release location as covariates to identify biological and geographic factors that may influence activity space ~ mass allometry in marine animals. In all models, Individual-level metrics of activity space and body mass were $\log_{10}$ transformed prior to model construction. Random intercept, random slope generalized linear models were fitted to obtain intercept (*a*) and scaling exponent (*b*) values for each combination of explanatory variable, with scaling relationships presented here in the form AS $= aM^b$, where AS indicates activity space (in square kilometers) and *M* indicates the mass of tagged individual (in grams).

All models and scaling relationships were constructed with a Markov chain Monte Carlo (MCMC) sampler accounting for correlated random effects arising from phylogenetic correlations between all species using the MCMCglmm package (Hadfield 2010) in the R statistical environment (R Core Team 2021). Model coefficients were estimated using diffuse prior specifications, with 10^4 MCMC iterations, thinned every 10 iterations with a burn-in value of 3,000. Model convergence was assessed using the Gelman-Rubin statistic. Measures of variance in models were quantified by calculating marginal and conditional coefficients of determination (R^2) using custom R scripts as formulated by Nakagawa and Schielzeth (2013). Marginal R^2 values provided the variance explained by the fixed effects in models, whereas conditional R^2 values provided the variance explained by the full model.

Phylogenetic correction in models were applied following methods described by Hadfield and Nakagawa (2010) by including a phylogenetic covariance matrix within models calculated using branch distances from published phylogenetic trees (henceforth indicated as "+ phylo" in formulas). The phylogenetic covariance matrix was generated using the inverseA function before applying it to each model using the ginverse parameter in the MCMCglmm function (Hadfield 2010). Taxonomic relationships between species for phylogenetic corrections was extracted from the Open Tree of Life (OTL) taxonomy database (https://tree.opentreeoflife.org). The OTL project assembles current phylogenetic relationships across all organisms on Earth by synthesizing published phylogenetic trees across multiple taxonomies (Hinchliff et al. 2015). The phylogenetic tree utilized in this study was built by subsetting the OTL data set for the species for which activity space data was available and combining results into a single phylogenetic tree (fig. S2; Udyawer 2022). Accessing the OTL data set, subsetting, and building the phylogenetic tree used in this analysis was conducted using the rotl R package (Michonneau et al. 2016). To allow for comparisons between taxonomic groups and with previous studies (e.g., Tamburello et al. 2015), model coefficients were used to predict the area of activity space, with estimated standard errors, for a 1-kg individual (AS_{1kg}, in square kilometers).

Activity Space ~ Mass Allometric Scaling

Allometric relationships were constructed to assess how activity space scales with body mass in marine animals. Allometric relationships were calculated (i) across all marine species combined ($\log_{10}(AS) \sim \log_{10}(M) +$ phylo), (ii) across each of the four marine taxonomic groups ($\log_{10}(AS) \sim \log_{10}(M) \times$ taxonomicgroup + phylo), and (iii) for each trophic group within each taxonomic group. To account for limited numbers of representative individuals

within some taxa-trophic groupings (e.g., marine reptiles) and facilitate comparisons with previous studies (Tamburello et al. 2015), we developed models on taxon-specific subsets ($\log_{10}(AS) \sim \log_{10}(M) \times$ trophicgroup + phylo). Model coefficient estimates and their associated standard errors were used to calculate marginal R^2 and AS_{1kg} values for each subset model.

Factors Influencing Activity Space ~ Mass Allometric Scaling

Two sets of models were used to assess how biological and geographic factors influence activity space ~ mass allometry in marine animals. First, a model selection framework was used where 16 candidate models were constructed to identify the most parsimonious combination of covariates that best explained variance in allometric scaling relationships. Candidate models were phylogenetically corrected additive models with all possible combinations of covariates (and mass as a constant variable in all models), including taxonomic group (t), trophic group (TG), foraging habitat (FH), and latitude of release site (Ltt; full model: $\log_{10}(AS) \sim \log_{10}(M) + t + TG + FH + Ltt + phylo$). Prior to model construction, a multicollinearity analysis using a Spearman's rank order correlation was conducted using the correlation R package (Makowski et al. 2020). A multilevel correlation structure was used with taxonomic group as a random effect to account for the lack of independence of observations within taxonomic groups. Collinearity testing highlighted that all variables used in subsequent models were not strongly correlated (Spearman coefficients < |0.5|; fig. S3). Candidate models were compared using a deviance information criterion (DIC) index (Spiegelhalter et al. 2002) using the MuMIn package (Bartoń 2020) in R, with the marginal R^2 estimated for each candidate model. Only main effects were considered in the model selection process. Variables present in the models with the lowest DIC score were regarded as influential biological or geographic factors.

Second, the influence of each covariate on allometric relationships was explored using a series of simple bivariate interaction models. All interaction models were built from the base phylogenetically corrected activity space ~ mass allometry model ($\log_{10}(AS) \sim \log_{10}(M) + phylo$), with the influence of taxonomic group ($\log_{10}(AS) \sim \log_{10}(M) \times t + phylo$), trophic group ($\log_{10}(AS) \sim \log_{10}(M) \times TG + phylo$), foraging habitat ($\log_{10}(AS) \sim \log_{10}(M) \times FH + phylo$), and release latitude ($\log_{10}(AS) \sim \log_{10}(M) \times Ltt + phylo$) tested. Intersect ($a$) and scaling exponent ($b$) coefficients with associated credibility intervals for each interaction term within models were estimated. DIC and conditional R^2 measures were estimated to assess the fit of each model, and how much of the variation in activity space ~ mass allometry was explained by in-

cluding each biological or geographic covariate. Model coefficients were also used to estimate AS_{1kg} values for each grouping of interaction terms to allow for within- and between-model comparisons.

Results

Scaling relationships for activity space with body mass over the complete data set showed positive correlations with an exponent of 0.64 (fig. 2; table 1). At the taxon level, teleosts displayed small scaling exponents for activity space (0.07; table 1), with secondary consumer fish species displaying a negative slope (−0.12), indicating that smaller secondary consumer fish species tended to display marginally larger activity spaces than larger species. Marine reptiles and rays displayed scaling relationships closer to the overall scaling relationship (marine reptiles = 0.57, rays = 0.55; fig. 2). Sharks displayed high scaling exponents (0.96) compared with other taxonomic groups and the 0.75 scaling exponent proposed by McNab (1963), indicating that metabolism is not the sole driver of this scaling relationship. Body mass alone explained 35% of variation in overall allometric scaling relationships (fig. 2; table 1).

Model comparisons across 16 candidate additive models showed that including taxonomic group (t), trophic group (TG), and release latitude (Ltt) in models explained the largest portion of variance in scaling relationships (44%; table 2), with the full model (explaining 43% variance) included within the first four best-fitting models. Release latitude was represented in the top eight most parsimonious models in scaling relationships (table 2). The allometric scaling exponent of species examined in the present study varied significantly with latitude, with species tagged in midlatitudes (between 20°S and 35°S) displaying scaling exponents closest to 1 (fig. 3), with teleosts displaying a high level of variability in allometric scaling across the full range of latitudes (fig. S4). Within the shark taxonomic group, species monitored at the northernmost (10°S–15°S) and southernmost (40°S–45°S) sites displayed negative scaling exponents compared with counterparts in midlatitudes (fig. 3). This is likely an effect of migratory or widely dispersing sharks (e.g., sandbar sharks, bull sharks, and dusky whaler sharks) being predominantly found and tagged in midlatitude sites.

Taxonomic group (t) was included as a covariate in the top two models (table 2), suggesting that allometric scaling of activity space for marine animals is taxon specific and significantly varies across latitudes. Trophic group (TG) was represented in the top four models, highlighting the influence of prey type targeted by tagged animals across the full size range and latitudinal gradient (table 2). Activity space scaling exponents of teleosts across the three trophic groups identified that second- and third-order consumers displayed
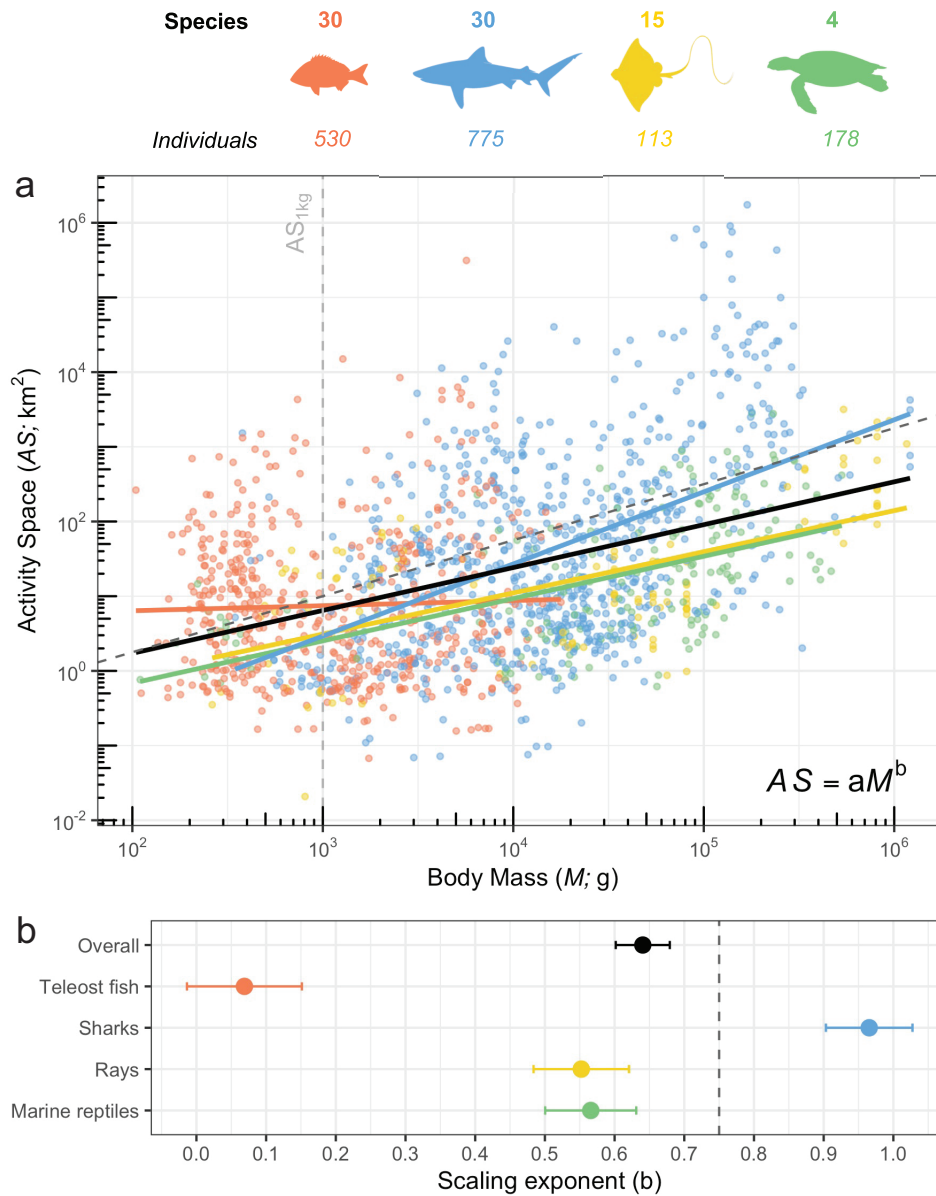
Figure 2: *a*, Allometry between log-transformed mass and activity space in marine animals tracked using the IMOS ATF continental-scale acoustic receiver network. The broken gray vertical line represents predicted activity space at 1 kg of mass (AS_{1kg}). *b*, Taxon-level scaling exponent values displayed for the full data set (black) and for the four major marine taxa (orange = teleost; blue = sharks; yellow = rays; green = marine reptiles) with 95% credible intervals represented. The broken black line in both panels represents the 0.75 body mass scaling exponent proposed by McNab (1963). Numbers of species and individuals within each taxa group used to create allometric relationships are shown at the top.

significantly lower scaling exponents (fig. 4) and potentially drive the overall scaling exponent (fig. 2). This pattern was likely driven by the large number of secondary consumer teleosts in the data set that displayed large activity spaces despite smaller body size (table 1). Predicted activity space for 1-kg individuals (AS_{1kg}) of secondary consumers was considerably larger than tertiary consumers (table 3; fig. S4).

Interaction models that assessed the effect of each biological and geographic covariate on allometric relationships showed that taxa and tagging location individually explained a larger proportion of the variance in scaling relationship than mass alone (table 3). Bivariate interaction models including release latitude explained the largest proportion of variance. However, the optimal additive

Table 1: Overall and taxon-level allometric scaling relationships between activity space (AS, in square kilometers) and body mass (M, in grams) in marine animals by trophic group

Taxonomic group, trophic group	n_{spp}	n_{ind}	a	b	Marginal R^2	AS_{1kg}
Overall	79	1,596	.27 (.19 to .37)	.64 (.61 to .68)	.35 (.16 to .38)	4.06 ± 2.58
Teleost fish:						
Overall	30	530	1.95 (1.51 to 2.51)	.07 (−.01 to .15)	.20 (.11 to .51)	7.47 ± 1.79
Primary	5	63	.31 (0 to .53)	.57 (.31 to .84)	.26 (.01 to .51)	3.66 ± 4.95
Secondary	13	294	3.96 (.01 to 12.3)	−.12 (−.2 to −.02)	.22 (.01 to .38)	10.2 ± 2.06
Tertiary	12	173	1.65 (.01 to 5.32)	.11 (−.08 to .31)	.19 (.01 to .42)	6.64 ± 4.37
Sharks:						
Overall	30	775	.09 (.06 to .12)	.96 (.90 to 1.02)	.34 (.15 to .59)	2.92 ± 1.82
Primary	...	...	...	...	...	...
Secondary	6	206	.16 (.01 to 3.85)	.81 (.68 to .93)	.31 (.11 to .63)	3.95 ± 3.09
Tertiary	24	569	.08 (.01 to 14.54)	1.01 (.92 to 1.07)	.43 (.20 to .64)	2.61 ± 2.09
Rays:						
Overall	15	113	.32 (.23 to .43)	.55 (.48 to .62)	.42 (.14 to .73)	3.14 ± 2.02
Primary	...	...	...	...	...	...
Secondary	14	109	.36 (.01 to .62)	.53 (.46 to .60)	.42 (.14 to .72)	3.57 ± 2.03
Tertiary	1	4	.06 (.01 to .09)	.77 (.56 to .98)	.74 (.34 to .99)	.29 ± 12.5
Marine reptiles:						
Overall	4	178	.27 (.20 to .37)	.57 (.50 to .63)	.38 (.11 to .68)	2.50 ± 2.01
Primary	1	50	.18 (.01 to .86)	.50 (.37 to .64)	.34 (.11 to .68)	.61 ± 4.02
Secondary	...	...	...	...	...	...
Tertiary	3	128	.40 (.05 to .82)	.55 (.46 to .61)	.44 (.16 to .74)	5.17 ± 1.89

Note: Scaling coefficients presented here are in the form $AS = aM^b$, with number of species (n_{spp}), number of individuals (n_{ind}), and marginal R^2 values for each relationship represented. Presented in parentheses for each model are 95% credible intervals for coefficients and marginal R^2. Predicted activity space at 1 kg of mass (AS_{1kg}, in square kilometers) with standard error is estimated for each taxonomic–trophic group combination.

Table 2: Model selection used to examine the influence of biological and geographic covariates on the allometric relationships between activity space and body mass across four major marine taxonomic groups

Rank	Model	df	Marginal R^2	DIC
1	AS ~ M + t + TG + Ltt	10	.44 (.14–.78)	4,568.55
2	AS ~ M + t + TG + FH + Ltt	11	.43 (.15–.77)	4,570.51
3	AS ~ M + TG + Ltt	7	.27 (.22–.33)	4,573.14
4	AS ~ M + FH + TG + Ltt	8	.28 (.22–.34)	4,575.47
5	AS ~ M + t + Ltt	8	.36 (.16–.77)	4,602.10
6	AS ~ M + Ltt	5	.26 (.20–.33)	4,602.23
7	AS ~ M + t + FH + Ltt	9	.42 (.15–.78)	4,603.85
8	AS ~ M + FH + Ltt	6	.26 (.19–.34)	4,604.37
9	AS ~ M + t + FH + TG	10	.41 (.12–.79)	4,678.96
10	AS ~ M + FH + TG	7	.26 (.17–.37)	4,678.99
11	AS ~ M + t + TG	9	.36 (.11–.76)	4,682.04
12	AS ~ M + TG	6	.26 (.18–.37)	4,682.27
13	AS ~ M + t + FH	8	.27 (.15–.68)	4,701.82
14	AS ~ M + FH	5	.26 (.16–.40)	4,702.09
15	AS ~ M + t	7	.32 (.14–.78)	4,705.17
16	AS ~ M	4	.35 (.16–.38)	4,705.33

Note: Presented within parenthesis for each model are 95% credible intervals for marginal R^2. All 16 candidate models displayed were ranked using a deviance information criterion (DIC) framework. All models were run using a Markov chain Monte Carlo sampler and phylogenetically corrected using species-level phylogeny (see fig. 1c for phylogeny used). AS = $\log_{10}$(activity space; km²); M = $\log_{10}$ (body mass; g); t = taxonomic group (teleost fish, shark, ray, reptile); TG = trophic group (primary, secondary, tertiary consumer); Ltt = release latitude; FH = foraging habitat (benthic, pelagic).
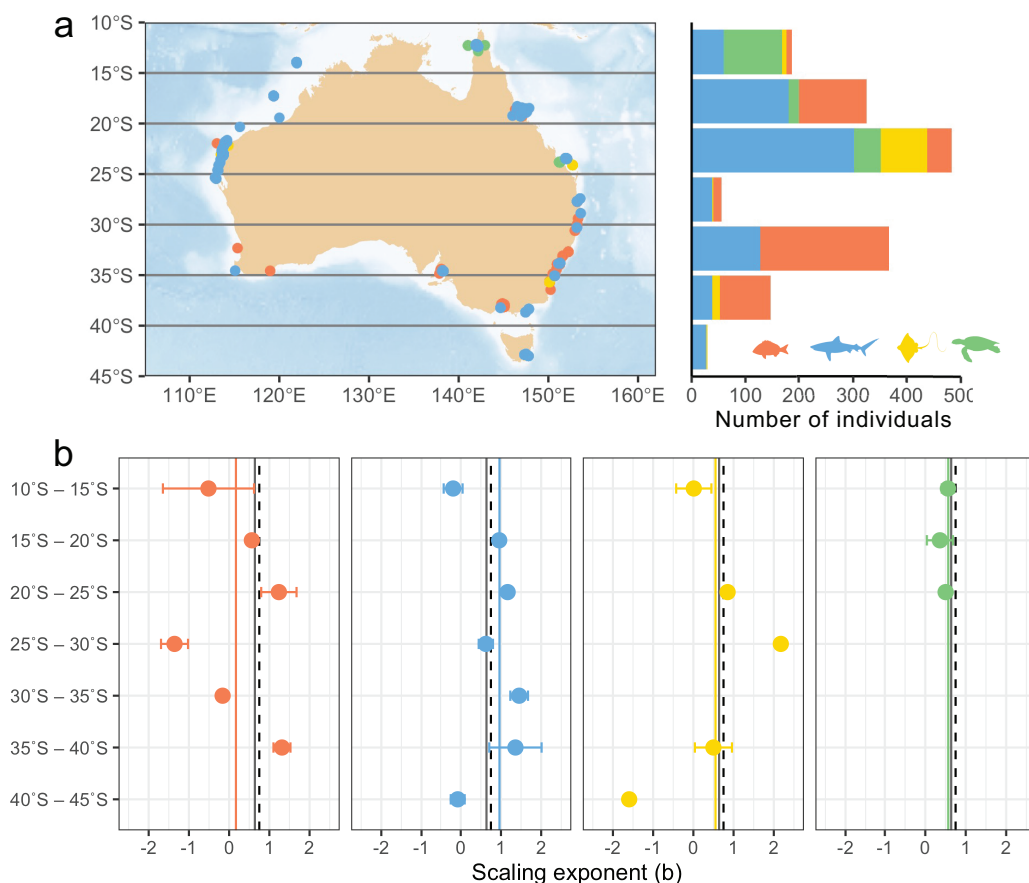
Figure 3: *a*, Release locations and numbers of individuals from each of the four major marine taxonomic groups monitored across 5° latitudinal subsets using the Integrated Marine Observing System's Animal Tracking Facility continental-scale network. *b*, Scaling exponent for subsets of individuals within each of the four major marine taxonomic groups (orange = teleost; blue = sharks; yellow = rays; green = marine reptiles) and within the seven latitudinal subsets represented as points with 95% credible intervals. The colored vertical line within each subpanel in *b* represents the overall taxon-level scaling exponent, the vertical black line represents the scaling exponent across the full data set, and the broken line represents the 0.75 body mass scaling exponent (McNab 1963).

model including taxonomic group and release latitude still outperformed models where both variables were used as interaction variables (table 3). The inclusion of trophic group as an interaction term reduced the amount of variability explained in the scaling relationship (table 3). This lower performance was likely due to the increased variation introduced by larger activity spaces of smaller secondary consumer teleosts in the data set.

Discussion

Analysis of continental-scale acoustic telemetry data for 79 marine species from four marine taxa revealed that marine animals exhibit allometric scaling for activity space very similar to terrestrial taxa, with an overall scaling exponent of 0.64. The latitude at which animals were tagged and their trophic group significantly influenced the allo-

metric scaling of activity space. In this study, all species were tracked using the same technology, and the metrics for activity space were computed for all tags using the same approach (Udyawer et al. 2018). This standardized methodology provided precise cross-taxa comparisons of allometric scaling. The use of discrete arrays of passive acoustic receivers may limit measurements of the full extent of some animals' activity space. However, we are confident that the large geographic footprint (spanning 32 degrees of latitude) of the receiver network augmented by the high number of animal location records ensured a good approximation of activity space for larger species while enabling the use of a consistent analytical method across a broad size range of species. The different values derived between this and previous studies (Nash et al. 2015; Tamburello et al. 2015; Rosten et al. 2016) highlight the complexity of natural systems and the ambiguity in allometric scaling relationships
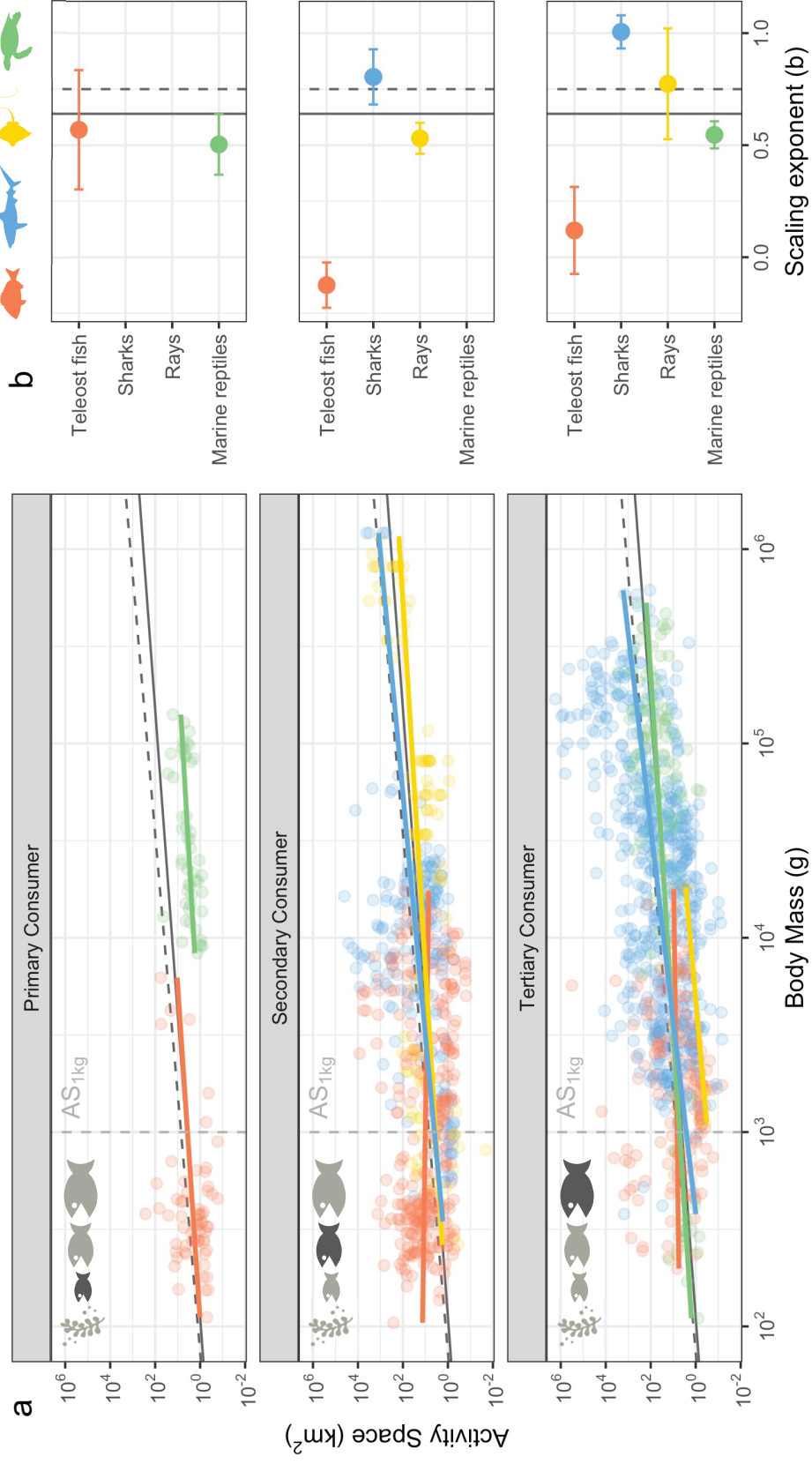
Figure 4: *a,* Allometry between log-transformed body mass and activity space tracked for four main marine taxa (orange = teleost; blue = sharks; yellow = rays; green = marine reptiles) across three trophic groups (primary, secondary, and tertiary consumers). The broken gray vertical line represents predicted activity space at 1 kg of mass (AS_{1kg}). *b,* Taxon-level scaling exponents with 95% credible intervals of each allometric relationships across the three trophic groups. The solid black line in all panels represent the allometric relationship and scaling exponent across the full data set, with the broken line representing the 0.75 body mass scaling relationship and exponent proposed by McNab (1963) as a comparison.

Table 3: Influence of biological and geographic variables on activity space ~ mass allometric scaling in marine animals

Model, variable	n_{spp}	a	b	Conditional R^2	DIC	AS_{1kg}
AS ~ M	79	.27 (.19 to .37)	.64 (.61 to .68)	.31 (.19 to .51)	4,705.33	4.06 ± 2.58
AS ~ M × t				.75 (.24 to .98)	4,633.07	
Taxon:						
Teleost fish	30	1.95 (1.51 to 2.51)	.07 (−.01 to .15)			7.47 ± 1.79
Sharks	30	.09 (.06 to .12)	.96 (.90 to 1.02)			2.92 ± 1.82
Rays	15	.32 (.23 to .43)	.55 (.48 to .62)			3.14 ± 2.02
Marine reptile	4	.27 (.20 to .37)	.57 (.50 to .63)			2.50 ± 2.01
AS ~ M × TG				.28 (.21 to .39)	4,642.47	
Trophic group:						
Primary	6	.73 (.04 to 15.03)	.24 (.04 to .44)			2.28 ± 7.32
Secondary	33	.95 (.79 to 1.13)	.34 (.29 to .39)			9.22 ± 1.51
Tertiary	40	.17 (.12 to .24)	.78 (.73 to .83)			3.75 ± 2.08
AS ~ M × FH				.32 (.20 to .52)	4,627.06	
Foraging habitat:						
Benthic forager	58	1.06 (.81 to 1.38)	.28 (.23 to .34)			7.95 ± 1.84
Pelagic forager	21	.04 (.01 to .10)	1.10 (1.03 to 1.16)			.96 ± 6.56
AS ~ M × Ltt				.29 (.21 to .43)	4,584.79	
Release latitude:						
10°S–15°S	9	2.06 (1.5 to 2.83)	.22 (.15 to .29)			23.88 ± 2.08
15°S–20°S	26	.12 (.08 to .19)	.80 (.72 to .88)			1.99 ± 2.63
20°S–25°S	30	.04 (.02 to .08)	1.02 (.97 to 1.07)			.58 ± 5.40
25°S–30°S	8	.15 (.07 to .29)	1.10 (.89 to 1.3)			22.67 ± 5.06
30°S–35°S	21	.78 (.44 to 1.39)	.47 (.32 to .61)			14.29 ± 3.75
35°S–40°S	12	.71 (0 to 1969.46)	.52 (.38 to .66)			16.21 ± 8.57
40°S–45°S	4	9.96 (2.33 to 42.55)	−.06 (−.21 to .1)			134.7 ± 28.2

Note: Scaling coefficients presented are in the form $AS = aM^b$, with numbers of species (n_{spp}), conditional R^2, and deviance information criterion (DIC) values for interaction models. Only simple uni- and bivariate interaction models were considered to identify the influence of each variable on activity space ~ mass allometric scaling. All models were run using a Markov chain Monte Carlo sampler and phylogenetically corrected using species-level phylogeny (see fig. 1c for phylogeny used). Presented within parenthesis are 95% credible intervals for coefficients for each model. Predicted activity space at 1 kg of mass (AS_{1kg}, in square kilometers) with standard error is estimated for each interaction model. $AS = \log_{10}$(activity space; km^2); $M = \log_{10}$(body mass; g); t = taxonomic group (teleost fish, shark, ray, reptile); TG = trophic group (primary, secondary, tertiary consumer); Ltt = release latitude; FH = foraging habitat (benthic, pelagic).

defined in marine systems. Here, we demonstrate the value of using individual-level measures (compared with summarized species-level measures), a consistent method of calculating activity space (e.g., smoothing parameters), and the utility of a coordinated continental-scale research infrastructure.

The overall scaling exponent derived from allometric scaling of activity space across marine taxa (0.64) was similar to that derived for terrestrial mammals and birds (fig. 5), but the exponent was substantially smaller than the 1.12–1.71 previously reported for marine fishes, in which activity space information was summarized using values derived from multiple published studies (Nash et al. 2015; Tamburello et al. 2015). We also found a very small scaling relationship in teleost fishes, which suggests that the allometric relationship in this taxonomic group is highly variable and not as strong as previously estimated (Tamburello et al. 2015). There are a number of possible reasons for this contrast with the published literature. First, we compared species across a much broader range of latitudes and habitat types

than used in previous studies. Nash et al. (2015) compared activity space only for coral reef fishes, which exist in a narrow latitude band (<30°) and inhabit the same habitat throughout their distributions (coral reef). Tamburello et al. (2015) deliberately omitted pelagic fish and instead selected only benthic fish, primarily perciform and scorpaeniform fishes. These tend to be slow-moving and sedentary species, again reducing the potential for interspecies variation. In our study, fish data were collected across a wide range of orders (30 teleost species within 18 orders), habitats, and temperature regimes. The broad range of teleost species examined here may have overridden any significant allometric effects of body mass on activity space found in previous studies and provides a more accurate picture of allometric scaling in teleost fishes.

Much of the literature around allometric scaling of activity space has been developed from location data collected for bird and mammal species (although see Hirt et al. 2017). In these groups, basal metabolic rate appears to be a good size predictor of activity space, and variation in allometric
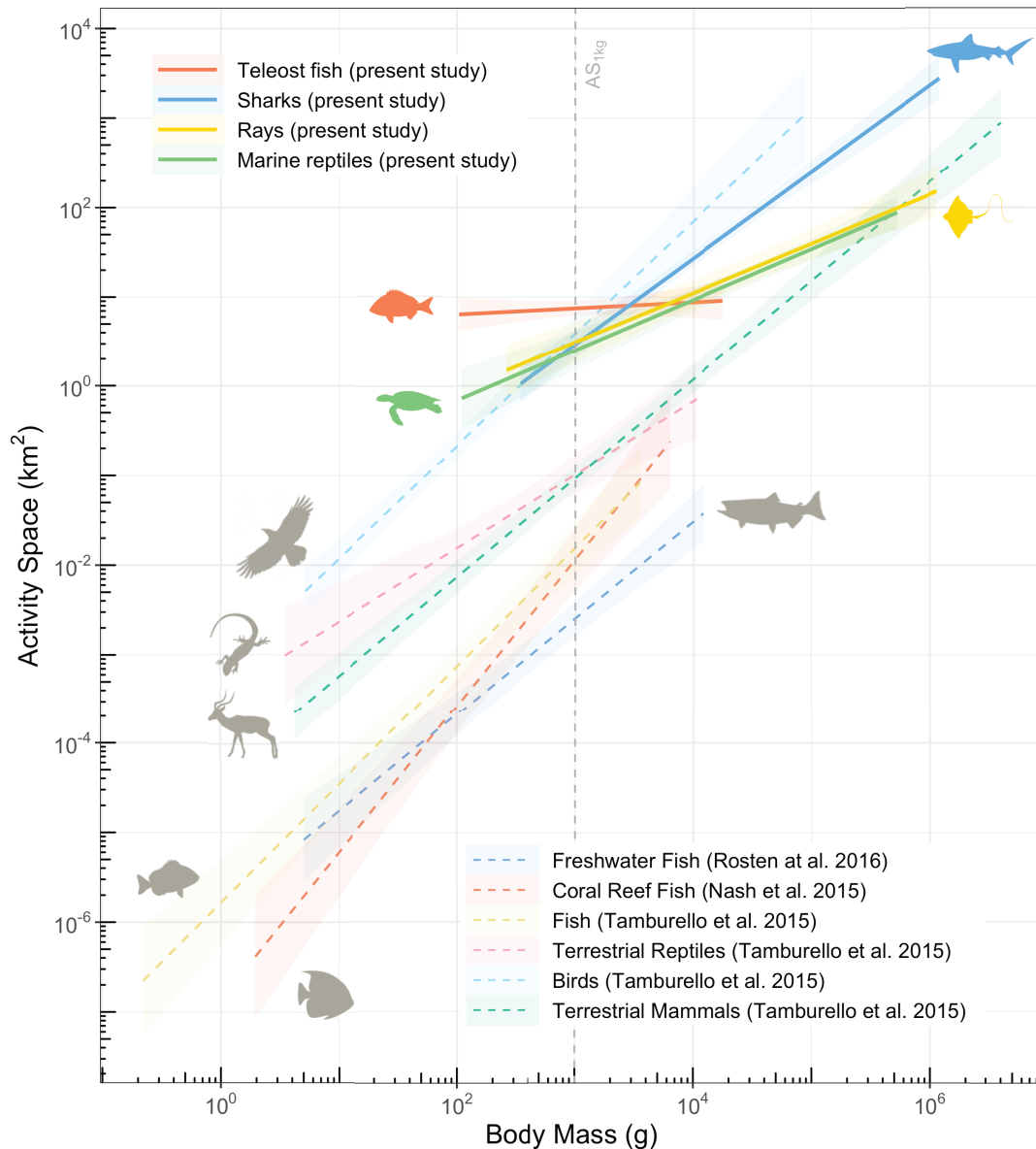
Figure 5: Allometric scaling relationships between activity space and body mass in four marine taxa from this study compared with scaling relationships from aquatic and terrestrial taxa from previous studies (Nash et al. 2015; Tamburello et al. 2015; Rosten et al. 2016). The broken gray vertical line represents predicted activity space at 1 kg of mass (AS_{1kg}). See table 1 for taxon-specific coefficients and marginal R^2 values for relationships from the present study.

scaling can be explained by factors such as geographical location, resource availability, habitat dimensionality, population density, and trophic level (Jetz et al. 2004). Here, we demonstrate that allometric scaling relationships of activity space across marine taxa are similar to that of terrestrial animals, with latitude and trophic group exerting a strong influence on activity space allometry across taxa. For many pelagic animals there is little or no decrease in mass-specific metabolic rate with body mass, and in many cases pelagic

animals have metabolic rates that scale proportionately (isometrically) rather than disproportionately (allometrically) to body mass (Glazier 2006). In the marine environment, it appears that metabolic scaling is not simply a function of body size and that additional ecological processes beyond energetic requirements also influence this relationship.

The latitudinal effect on activity space allometry observed in this study likely reflects the influence of other factors that correlate with latitude (e.g., temperature, productivity).

Seasonal changes in temperature often drive specific be-haviors in animals and modify movement patterns (Fiedler et al. 2021); therefore, animals in areas with greater sea-sonal change or species with highly seasonal behaviors (i.e., breeding or feeding) are expected to have more vari-able allometric scaling relationships between seasons. Pre-vious metabolic scaling theories show that temperature-dependent metabolic performance is highly conserved across taxa and environments (Savage et al. 2004), with metabolic rates generally higher at warm temperatures (Huey and Kingsolver 1989; Gillooly et al. 2001; Payne et al. 2016). Ecto-thermic organisms might be expected to increase foraging and activity space at warmer temperatures to meet higher metabolic and energetic demands until critical thermal thresh-olds are reached. In the present study, animals tagged at warmer latitudes generally displayed larger activity spaces than those observed in more temperate species (fig. S4). This reflects similar trends seen in the range extent of animals, where the breadth of a species' environmental tolerance reflects the variability of the environment (the climate vari-ability hypothesis; Stevens 1989; Pintor et al. 2015).

Productivity and density of food can particularly influ-ence the size of the area used by animals (Lindstedt et al. 1986; Smith et al. 2013; Tucker and Rogers 2014). Species mostly occurring at localized regions of very high food avail-ability at low latitudes (e.g., coral reefs) would be expected to have smaller activity space than species that inhabit broader regions in temperate or pelagic areas where food resources are patchier and more dynamic (Harcourt et al. 2002; Benoit-Bird and McManus 2012; Carroll et al. 2016). Since many of the species from low latitudes were tagged at coral reefs that are composed of isolated reef systems, habitat fragmenta-tion might have further constrained the area used by some tropical species (Espinoza et al. 2015; Momigliano et al. 2015). Additionally, the relative lack of tracking infrastruc-ture and tracking studies across the north and south coasts, compared with the east and west coasts of Australia, may have had a potential effect on the longitudinal relationship, with more exaggerated scaling effects expected in species occurring at the extremities of the latitudinal scale.

Our findings provide limited support for earlier studies that showed an increase in activity space allometry with tro-phic position in marine taxa (Tamburello et al. 2015). As high-trophic-level organisms typically feed on resources that are sparsely distributed, mobile, and unpredictable across the landscape, such species typically require a large home range (Kelt and Van Vuren 2001; Carbone et al. 2007; Jaine et al. 2014; Tucker and Rogers 2014). In our study, activity space allometry of tertiary consumers was lower than that of secondary consumers. Such discrepancies might be related to a range of mechanisms that were not examined in previ-ous studies because of a small number of taxa across trophic position and limited spatial range.

1. *Foraging strategy*. Many secondary consumers can be considered patch foragers, while many benthic marine ter-tiary consumers use a sit-and-wait strategy (Webb 1984). The latter strategy means that tertiary consumers can optimize energy intake by reducing foraging costs (e.g., searching) compared with actively foraging across patchily distributed resources (Carbone et al. 1999; Thompson and Fedak 2001). The effect of feeding strategy on activity space has previously been shown for estuarine crocodiles (*Crocodylus porosus*) that transition ontogenetically from a highly active foraging mode that exploits estuarine prey to a less active sit-and-wait feeding strategy focused on killing terrestrial ungulates along riverbanks (Hanson et al. 2015). Similarly, social hier-archy and territorial interactions among individuals may influence activity space, where the larger dominant individ-uals maintain discrete territories, whereas the smaller subor-dinates move over much larger areas (Campbell et al. 2013).

2. *Dimensionality of foraging habitat*. Differences in the dimension of foraging habitat have been shown to affect ac-tivity space (Pearce et al. 2013; Sequeira et al. 2018) and to lower exponents of the body mass–home range relationship in mammals (Carbone et al. 2004). As the present study es-timated two-dimensional activity space, it might have also underestimated the true home range of tertiary consumers species that feed in a three-dimensional habitat (Bestley et al. 2015; Udyawer et al. 2015; Lee et al. 2017).

3. *Resource quality*. Space required by an organism to meet its metabolic needs is partly determined by resource supply, which is affected by both resource abundance and quality (Yeager et al. 2014). When comparing across tro-phic groups, species consuming higher-quality prey (e.g., tertiary consumers) often feed less frequently than species that consume lower-quality resources (e.g., primary con-sumers; Arrington et al. 2002; Vinson and Angradi 2011). One mechanism by which species may compensate for lower-quality food is by increasing the quantity of food resources consumed. This would likely result in greater activity space needed to source more food and maintain similar levels of energy balance and growth. Conversely, species occupying highly productive habitats may not have a requirement to move far to acquire adequate food and shelter resources than in otherwise lower-quality habitats (Pillans et al. 2017, 2021).

4. *Antipredatory behavior*. The extent of activity space is not solely driven by foraging and could be a result of animals making movement decisions to minimize preda-tion risk. Secondary consumers are likely to be more prone to this influence while trying to meet energy demands (Brown 1988; Heithaus et al. 2002; Laundré 2010; Mitchell and Harborne 2020).

While other factors might be affecting activity space variations across trophic groups (e.g., seasonality in move-ments, reproduction), the mechanisms described above may

all contribute to larger and more variable activity spaces and dispersal capacities in secondary consumers than tertiary consumers. In addition to these factors, there are likely other mechanistic drivers of inter- and intraspecific variability in allometries that have not been considered here (e.g., nonlinear allometry) but should be considered in future meta-analytical approaches to further understand inter- and intraspecific variation in activity space ~ mass allometric relationships across marine taxa.

An important consideration inherent to allometric scaling studies is the method used to collect data and compute the scaling factors. Macroecological relationships requiring empirical data spanning multiple species and across large geographical scales often rely on numerous species- or location-specific work conducted across a wide community of researchers (e.g., Ellis et al. 2019; Lowerre-Barbieri et al. 2021). While allometric scaling relationships have previously been derived using diverse data sources (e.g., Nash et al. 2015; Tamburello et al. 2015), there are likely unavoidable biases in doing so, as acknowledged by the authors of these studies. The approach used in our study reduces these uncertainties and provides robust estimates by restricting estimation of activity space to a single technology (passive acoustic telemetry) and simultaneously applying a standardized analysis across all taxa (e.g., same smoothing factors). The IMOS continental acoustic telemetry network has now been successfully used to identify intra- and interspecific functional movement behaviors (Brodie et al. 2018), stock structure of commercially important marine species (Lédée et al. 2021), and impacts of changes in human activity on animal populations during global disruptions such as the COVID-19 pandemic (Huveneers et al. 2021). However, as with all technology, there are inherent limitations to using data derived from acoustic telemetry to estimate a species activity space. First, acoustic telemetry is not suited to tracking movements of all aquatic species (Hussey et al. 2015; Harcourt et al. 2019). Second, acoustic receivers can have variable detection ranges, influenced by a variety of factors including transmitter power output, biofouling, ambient noise, and environmental conditions (Heupel et al. 2008; Kessel et al. 2014; Huveneers et al. 2016, 2017). Finally, infrastructure deployments across the continent and within individual acoustic telemetry networks can vary in space and time according to active research projects, with smaller arrays potentially introducing a bias in underestimating activity spaces for some species that move over larger distances than that being covered by the continental network (Steckenreuter et al. 2017).

The use of unifying models to understand how animals occupy space can provide important information on population structure and distribution of species across landscapes and seascapes. Many of these unifying models have been tested primarily in terrestrial and freshwater systems, where there are many fine-scale and long-term data on animal movements. In marine ectotherms, a hierarchical approach to examining allometric scaling exponents reveals a more complex relationship between body mass and activity space across taxa, trophic groups, and foraging behaviors. Here, we demonstrated the utility of collaborative passive telemetry networks to assess activity space–body mass allometry in a range of marine taxa and across a wide geographic scale, an approach not previously feasible because of the difficulty of obtaining long-term and standardized metrics of activity space over biologically relevant spatial scales.

Statement of Authorship

Conceptualization: V.U., C.H., F.J., R.C.B., X.H., H.A.C., S.B., R.G.H., C.A.S., M.R.H.; funding acquisition: F.J., R.G.H., C.A.S., M.R.H.; methods development: V.U., X.H., F.J., C.H., C.A.S., M.R.H.; data collection: V.U., C.H., F.J., R.C.B., S.B., H.A.C., R.G.H., X.H., E.J.I.L., C.A.S., M.D.T., A.A., A.B., C.B., B.B., P.A.B., G.C., L.I.E.C., L.C.-R., A.F., D.H., A.R.H., N.A.K., K.L., M.L., M.L., T.M., J.M., J.D.M., R.M., F.M., M.M., K.M., B.M.N., B.O., N.L.P., V.P., T.P., R.D.P., R.D.R., P.R., J.M.S., A.S., C.W.S., D.v.d.M., M.R.H.; data analysis: V.U., X.H., M.-J.B., F.J., C.H.; data validation: V.U., X.H., F.J., C.H.; writing original draft: V.U., V.H., F.J., R.C.B., S.B., M-J.B., H.A.C., X.H., C.A.S., M.D.T., M.R.H.; review and editing: V.U., C.H., F.J., R.C.B., S.B., H.A.C., R.G.H., M-J.B., X.H., E.J.I.L., C.A.S., M.D.T., A.A., A.B., C.B., B.B., P.A.B., G.C., L.I.E.C., L.C.-R., A.F., D.H., A.R.H., N.A.K., K.L., M.L., M.L., T.M., J.M., J.D.M., R.M., F.M., M.M., K.M., B.M.N., B.O., N.L.P., V.P., T.P., R.D.P., R.D.R., P.R., J.M.S., A.S., C.W.S., D.v.d.M., M.R.H.

Data and Code Availability

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