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RESEARCH

Ontogenetic scaling of disc width with total length in west African batoids

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Abstract

Morphological scaling describes changes in the size or shape of one morphological character (e.g. mass, length, width, area etc.) as another increases in size. Understanding how morphological characters scale with body size can shed light on how natural selection influences morphology, and the nature of ecomorphological relationships through ontogeny. Batoids (Elasmobranchii: Batoidea) are a highly specialised lineage of cartilaginous fishes displaying extreme dorsoventral flattening. Despite this, little is known about morphological scaling in batoids compared to sharks. In this study we test the relationship between disc width and total length in five batoid species (*Torpedo torpedo*, *Mobula tarapacana*, *Fontitrygon margarita*, *Raja parva*, *Rhinobatos irvinei)* representing four orders that differ in both ecology and morphology, measured from artisanal fisheries in Western and Central Ghana. Whilst a lack of existing ecological data presents some limitations, our results are broadly consistent with ecomorphological theory previously applied to sharks. Moreover, we find that for some lineages (including some myliobatiform taxa) total length may represent a valid proxy for estimating overall body size. This finding has applications for body size and shape estimation in partially processed batoids obtained from fishing camps, and extinct taxa known only from incomplete or fragmented remains.

Keywords Elasmobranchii · Stingray · Rays · Allometry · Isometry · Body size

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Introduction

Morphological scaling relationships underpin phenotypic diversity at both the interspecific and ontogenetic levels (Schmidt-Nielsen 1984; Brown and West 2000). These relationships are typically defined as either allometric or isometric. Allometry describes disproportionate (as opposed to proportionate with isometry) change in the size/rate of some morphological characteristic or physiological process relative to another (Schmidt-Nielsen 1984), and is thought to occur when the different species/life stages are subjected to different selective pressures or evolutionary constraints (Voje et al. 2014). Studying the scaling relationships of morphological characteristics is important as it can provide valuable insight into form-function relationships and the nature of selection acting upon morphology relative to ecology (Voje et al. 2014). This in turn can enhance our understanding of the factors underlying the evolution of morphological diversity (or lack thereof) both between species and across ontogeny (Voje et al. 2014). Additionally, an understanding of how different morphological traits scale with increasing body size is important from a palaeontological perspective, as scaling relationships in extant groups are often used as the basis of body size predictions in extinct species (Reynolds 2002; Gayford et al., 2024; Engelman 2022).

Batoids (Elasmobranchii: Batoidea) are an ecologically important and morphologically diverse group of cartilaginous fishes distributed globally in marine and freshwater ecosystems (Last et al. 2016; Flowers et al. 2021). The defining characteristic of batoids is extreme dorsoventral compression, with most groups also exhibiting a pectoral ‘disc’ formed through the attachment of the pectoral fins to both the body and rostrum (Fontanella et al. 2013; Last et al. 2016). Most extant batoids use this disc as the primary source of thrust generation with the tail primarily being used as a defensive appendage. However, in some species, including rhinopristiform and torpediniform taxa, body caudal fin (BCF) locomotion (also known as axial undulatory locomotion) is used, with the pectoral fins likely used to enhance manouvreability (Schaefer and Summers 2005). Whilst a number of recent studies have addressed morphological scaling relationships in sharks (e.g. Irschick and Hammerschlag 2015; Bellodi et al. 2023; Gayford et al. 2023b; Seamone et al. 2023), batoids have been neglected in spite of their unusual body form. The few studies that have explicitly investigated scaling of morphological characters (as opposed to performance-based characters, e.g. Kolmann et al. 2018; internal anatomy, e.g. Lisney et al. 2017; or length-weight relationships, e.g. Lteif et al. 2016) in batoids do not provide rigorous statistical tests for allometric growth (El Kamel-Moutalibi et al. 2013; Yeldan and Gundogdu 2018). Hence, we have very little understanding of how different aspects of batoid morphology scale with body size either through ontogeny or between species. This limits our ability to understand the adaptive basis of morphological (and locomotor) variation and potentially affects the validity of body size estimates in extinct batoids.

In this study we uncover ontogenetic scaling trends between disc width and total length in 5 species representing all 4 extant batoid orders: *Torpedo torpedo* (Torpediniformes), *Mobula tarapacana* (Myliobatiformes), *Fontitrygon margarita* (Myliobatiformes), *Raja parva* (Rajiformes), and *Rhinobatos irvinei* (Rhinopristiformes). Disc width (the maximum diameter of the pectoral disc) and total length (the distance from the tip of the snout to the tip of the tail) are the most common proxies for body size in batoids, however little empirical data exists regarding the relationship between these two measurements through ontogeny or among species. We address what the nature of allometry/isometry may imply about the ecology of each species (drawing from ecomorphological theory previously applied to selachian elasmobranchs), and the extent to which total length correlates with body size. We hypothesise, on the basis of variation in the primary function of the tail (thrust generation vs. defence appendage), that disc width and total length will not be tightly correlated, at least in species that use paired/median fin locomotion. However, if this hypothesis is rejected, it suggests that total length could be a valuable proxy for disc width (and vice versa) and body size in the absence of other data. We also suggest potential avenues for future research, given the paucity of studies addressing scaling relationships in batoids.

Methodology

Data collection

Data on batoid landings were collected for three days per week from October 2022 to April 2024 from four different artisanal fishing communities in western and central Ghana (Fig. 1). All specimens were caught in drift and bottomset gillnets, and taxonomic and morphometric data was collected by trained volunteers prior to processing by fishers. The specimens encountered were identified to the lowest possible taxonomic resolution using keys from Séret (2006), Compagno (2002), and Séret (2016). The total length to the nearest cm was measured as the distance between the tip of the snout and the tip of the tail (defined as the tip of the upper caudal lobe for *R. irvinei* and *T. torpedo*, in which two lobes can clearly be distinguished). Disc width to the nearest cm was measured as the maximum diameter of

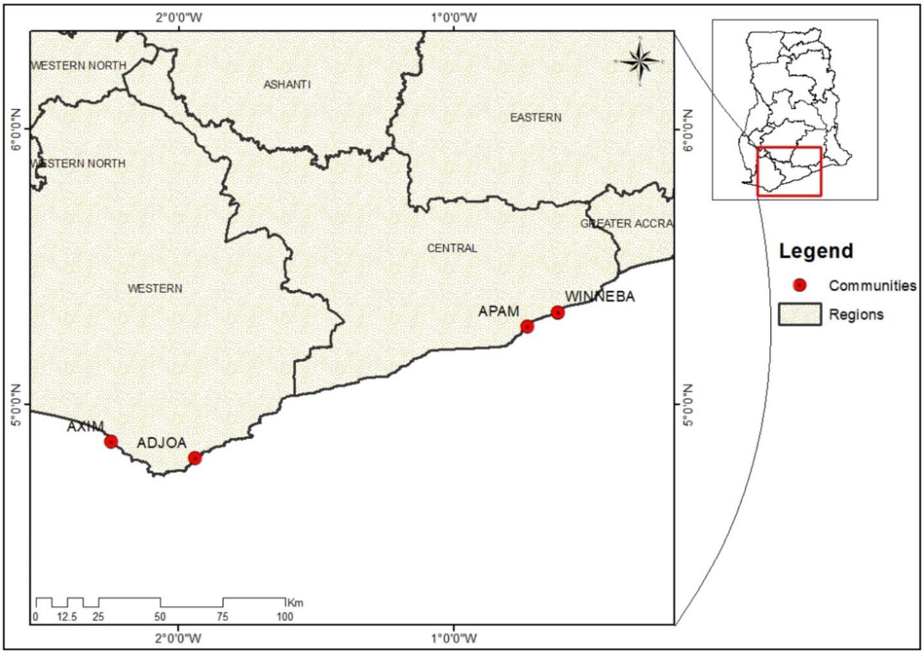

Fig. 1 Map of Ghana showing Western and Central regions, with the four study communities. Adapted from Seidu et al. (2022)

the pectoral disc (Fig. 2). Sex of individuals were recorded based on the presence/absence of claspers (male intromittent organs), which are visible from an early stage of development protruding from the medial edge of the pelvic fins (Capapé, and Zaouali 1994). Due to the heavily time-constrained nature of sampling in artisanal fishing communities, it was not possible to estimate measurement error or potential post-mortem changes in morphology.

The final dataset consisted of 215 individuals, including males, females, adults and juveniles of all five species. The full log-transformed dataset can be found in the online supplementary materials associated with this article. Data were obtained for a total of 21 *T. torpedo* with disc width ranging from 7 to 31 cm and total length ranging from 12 to 44 cm, 26 *M. tarapacana* with disc width ranging from 48 to 354 cm and total length ranging from 40 to 430 cm, 39 *F. margarita* with disc width ranging from 11 to 43 cm and total length ranging from 19 to 110 cm, 95 *R. parva* with disc width ranging from 6 to 46 cm and total length ranging from 11 to 71 cm, and 34 *R. irvinei* with disc width ranging from 9 to 42 cm and total length ranging from 66 to 125 cm.

Data analysis

Prior to data analysis, disc width and total length values were log transformed so that the scaling exponent could be calculated as the slope of a linear relationship: $\text{LogY}=\text{LogA}+\text{b}\cdot\text{LogX}$, where Y is the disc width, A is the intercept, X is the total length, and b is the scaling exponent. The full log transformed dataset can be found in the online supplementary material associated with this article. To calculate correlation between total length and disc width in batoids, we fit a series of simple linear regression models in R (R Core Team, 2024). Ordi-

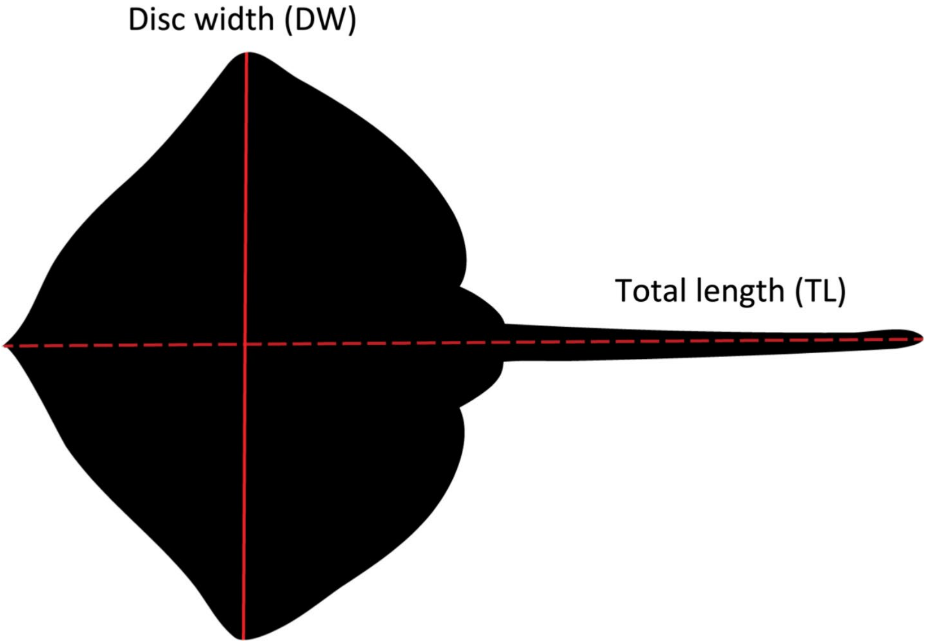

Fig. 2 Disc width (solid line) and total length (dashed line), as measured on *R. parva*. Note that for species with two defined caudal lobes (*R. irvinei* and *T. torpedo*), the tip of the tail is defined as the tip of the upper caudal lobe, as outlined in the above text

nary least squares (OLS) regression was used following previous studies (e.g., Gayford et al. 2023b; Irschick and Hammerschlag 2015). Three models were fit per species: one for each sex, and a third model pooling males and females together. This was done as previous studies have reported marked sexual dimorphism in morphological scaling relationships for other elasmobranch species (Gayford et al. 2023a). Sex-based regression models were not fit for *Torpedo torpedo* due to an insufficient sample size. The gradient of each of these regression analyses indicates the nature of the scaling relationship, with gradients of 1 equating to isometric growth, and gradients significantly greater or lower than 1 equating to positive or negative allometric growth, respectively.

Results

Full results (males and females pooled)

Disc width scales isometrically with total length in *T. torpedo* (Fig. 3a), *M. tarapacana* (Fig. 3b) and *Raja parva* (Fig. 3d), and in each case the relationship is relatively strong, with R^2 ranging from 0.69 to 0.90 (Fig. 3; Table 1). In *F. margarita* (Fig. 3c) and *R. irvinei* (Fig. 3e) disc width scales with negative allometry, becoming disproportionately narrower as total length increases (Fig. 3; Table 1). In these species the relationship between disc width and total length is much weaker, with R^2 ranging from 0.02 to 0.48 (Table 1).

Female results

Disc width scales isometrically with total length in females of all species other than *F. margarita* (Fig. 4b), in which disc width scales with negative allometry (Fig. 4; Table 2). R^2 varies from 0.86 to 0.10, being highest in *M. tarapacana* (Fig. 4a) and lowest in *R. irvinei* (Fig. 4d; Table 2).

Male results

Disc width scales isometrically with total length in male *M. tarapacana* (Fig. 5a) and *Raja parva* (Fig. 5c), with associated R^2 values of 0.54 and 0.79 respectively (Fig. 5; Table 3). In male *F. margarita* (Fig. 5b) and *R. irvinei* (Fig. 5d) disc width scales with negative allometry, becoming disproportionately narrower as total length increases (Fig. 5; Table 3). In these species R^2 values range from 0.61 to -0.07 (Table 3). Notably, the slope for *R. irvinei* does not differ significantly from 0 (Table 3), suggesting in males that there is no relationship whatsoever between disc width and total length.

Discussion

Our results indicate that both total length and disc width might provide a reasonable proxy for body size in at least some batoid orders, even where only one of these measures is traditionally used in the literature (Tables 1, 2 and 3). Whilst total length is the morphologi-

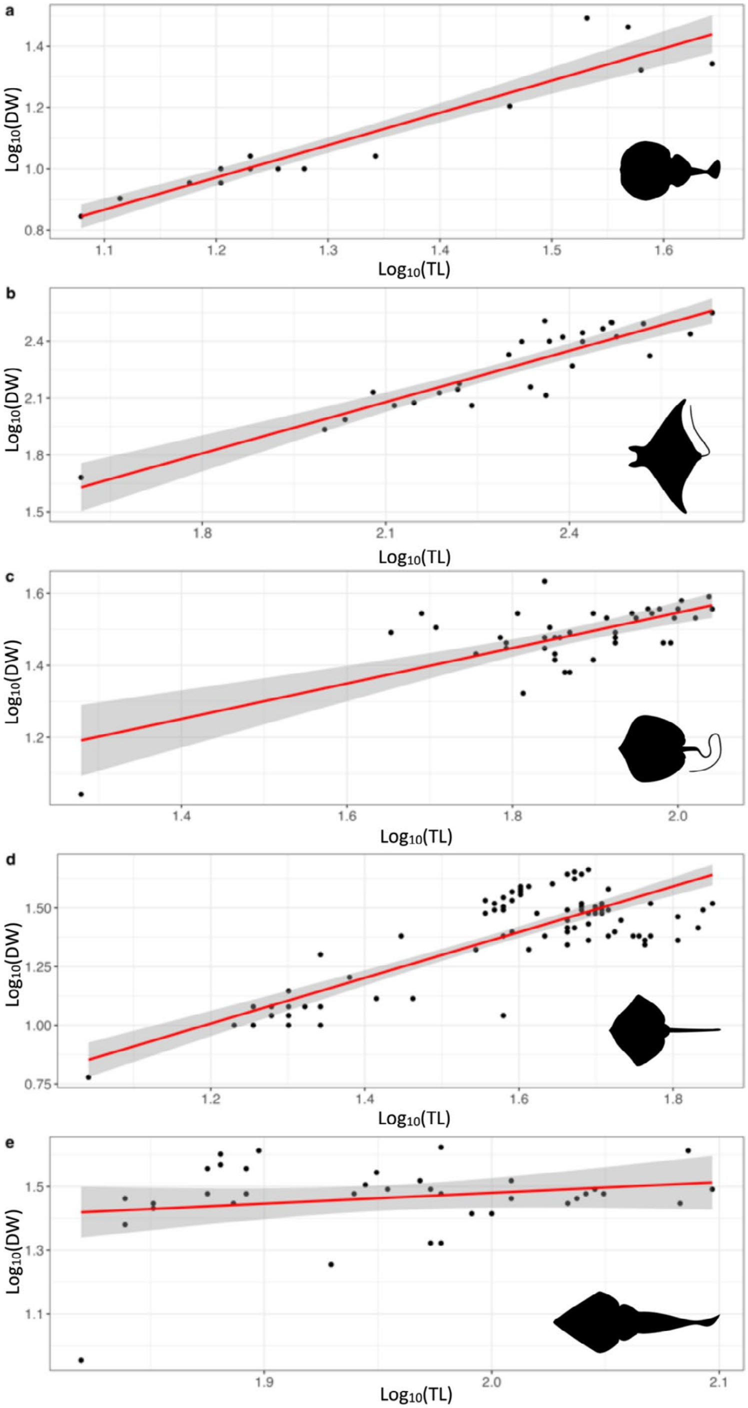

Fig. 3 scaling relationships between total length (TL) and disc width (DW) in *T. torpedo* (**a**), *M. tarapacana* (**b**), *F. margarita* (**c**), *R. parva* (**d**), and *R. irvinei* (**e**). Silhouettes are for illustrative purposes only and are not drawn to scale

Table 1 Scaling relationships between total length and disc width for each batoid species. Results that differ significantly from isometric expectations ($p < 0.05$) are indicated in bold

Species	*N*	Intercept (+/- SE)	Coefficient (+/- SE)	T	*P*	Adjusted R^2	F
T. torpedo	21	-0.29142 ± 0.095	1.05271 ± 0.074	0.711	0.485	0.901	201.9
M. tarapacana	26	0.18662 ± 0.194	0.90098 ± 0.084	1.180	0.247	0.810	116.1
F. margarita	**39**	**0.56227 ± 0.150**	**0.49169 ± 0.080**	**6.349**	**1.7e-07**	**0.479**	**37.8**
R. parva	95	-0.16078 ± 0.105	0.97344 ± 0.066	0.399	0.691	0.689	213.5
R. irvinei	**34**	**0.8061 ± 0.501**	**0.3370 ± 0.256**	**2.589**	**0.014**	**0.021**	**1.732**

cal character most commonly used to approximate body size in selachian elasmobranchs, Torpediniformes, Rhinopristiformes, and Rajiformes, this is not the case in myliobatiform batoids. The flattened and wide span of the myliobatiform pectoral disc has led to disc width widely being considered the most appropriate morphological proxy for overall body size in this lineage (Froese and Pauly 2010; Pimiento et al. 2019). In line with this consensus, and our initial hypothesis, we found that disc width and total length are at best weakly correlated in *F. margarita* (and *R. irvinei)* (Figs. 3 and 4; Tables 1, 2 and 3). However, this was not the case for the remaining three species, in which correlation between disc width and total length was strong and did not deviate from isometric predictions (Figs. 3, 4 and 5; Tables 1, 2 and 3). This indicates that in some taxonomic groups (namely Torpediniformes, Rajiformes and Mobulidae) total length and disc width may provide valid proxies for one another and indeed for overall body size estimation. This is notable given that disc width is not typically used to denote body size in Torpediniformes or Rajiformes, and that Mobulidae belongs to the order Myliobatiformes, in which disc width is the only commonly used proxy for body size (Last et al. 2016). Interestingly, our results also indicate that the distinction between body caudal fin (axial undulatory) locomotion (in *R. irvinei* and *T. torpedo*) and median/paired fin locomotion (in *F. margarita* and *M. tarapacana*) is not important in driving scaling of disc width, as both isometry and allometry are recovered from both categories. Many fisheries targeting batoid species process catch prior to landing, in some cases removing the pectoral fins and/or tail from the body (Curtis and Sosebee 2015; Almeida Marques et al. 2020). Thus, upon landing, accurate body size estimation by researchers using disc width alone would be difficult in many circumstances. However, strong correlation between disc width and total length provides a promising avenue through which this issue could be overcome, enabling the collection of vital biological data from poorly studied or threatened species. For similar reasons, strong correlation between disc width and total length is highly relevant in a palaeobiological context. Many extinct chondrichthyan species (including taxa belonging to Torpediniformes, Rajiformes and Mobulidae – the species we found to display relatively strong relationships between total length and disc width) are known only from incomplete remains (Adnet et al. 2012; Marramà et al. 2018, 2019), making accurate reconstructions of body size and shape challenging. Fully intact specimens with complete tails and pectoral discs are rare, and hence finding alternative morphological proxies through which body size and shape can be reconstructed is of great importance. Our results show that a tight relationship between disc width and total length cannot be assumed, but that in some species it may be valid. For this reason, additional studies incorporating more species are warranted so that we can develop a better understanding of the lineages for which both total length and disc width might provide valid proxies for body size.

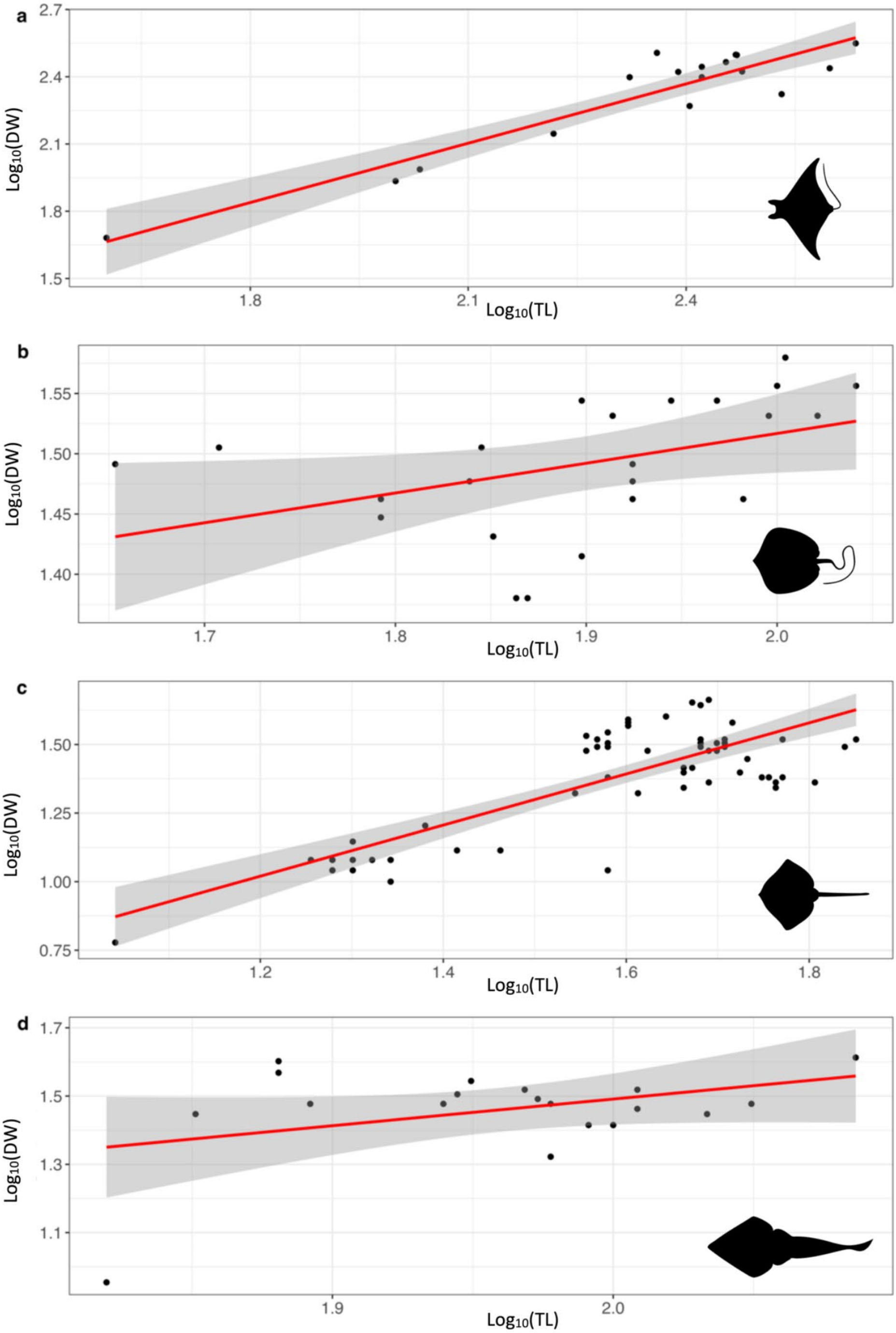

Fig. 4 scaling relationships between total length (TL) and disc width (DW) in female *M. tarapacana* (**a**), *F. margarita* (**b**), *R. parva* (**c**), and *R. irvinei* (**d**). Silhouettes are for illustrative purposes only and are not drawn to scale

Table 2 Scaling relationships between total length and disc width for female individuals only of each batoid species. Results that differ significantly from isometric expectations are indicated in bold

Species	*N*	Intercept (+/- SE)	Coefficient (+/- SE)	T	*P*	Adjusted R^2	F
M. tarapacana	15	0.25093 ± 0.207	0.88213 ± 0.088	1.339	0.201	0.8613	100.3
F. margarita	**21**	**1.0228 ± 0.2126**	**0.2470 ± 0.1119**	**6.732**	**1.17e-06**	**0.1498**	**4.876**
R. parva	60	-0.09808 ± 0.15067	0.93168 ± 0.09429	0.725	0.472	0.613	97.63
R. irvinei	17	-0.07088 ± 0.88247	0.78102 ± 0.45006	0.487	0.633	0.1005	3.011

Whilst the inclusion of only two morphological characters in this study and a lack of ecological information available regarding our target species impedes our ability to provide a thorough discussion of ecomorphology, our results are broadly consistent with the allometric niche shift hypothesis. This hypothesis states that allometry is more likely to be observed in species exhibiting clear ontogenetic shifts in trophic and/or spatial ecology (Gayford et al. 2023b). Within this framework, an isometric relationship between disc width and total length in both *T. torpedo* and *M. tarapacana* (Figs. 3, 4 and 5; Tables 1, 2 and 3) is logical, as existing studies suggest there are no significant ontogenetic shifts in diet or habitat usage in these species (El Kamel-Moutalibi et al. 2013; Stewart et al. 2017; Tiralongo et al. 2019). Therefore, isometric scaling is expected in the absence of shifts in trophic or spatial ecology, because selection acting upon morphology will remain constant through ontogeny. It should be noted that isometric growth can still result in functional shifts through ontogeny (Seamone et al. 2023), and so even if the disc of adult rays is geometrically identical to that of juveniles, intrinsic changes to locomotor function may result due to the scaling relationships of linear and area dimensions relative to mass. Regrettably, little to no ontogenetic information exists regarding the ecology of *R. parva*, *F. margarita* or *R. irvinei* (Froese and Pauly 2010). The apparent lack of relationship between disc width and total length in *R. irvinei* (Table 1; Fig. 3) might suggest a functional shift towards body and caudal fin (BCF) locomotion through ontogeny, placing less functional importance on progressively smaller pectoral fins. This morphological shift would theoretically favour steady swimming over manoeuvrability, an ontogenetic trend observed in several shark species (Gayford et al. 2023a). However, in the absence of additional functional and ecological data it is difficult to speculate as to why this might be the case in *R. irvinei*. The only sex-based scaling difference in our results was that of *R. irvinei*, in which disc width scales isometrically in females but with negative allometry in males (Figs. 4 and 5; Tables 2 and 3). However, the low R^2 values for these regressions (Tables 2 and 3) precludes further ecomorphological inference.

Conclusion

Our understanding of morphological scaling in batoids is poor compared to selachian elasmobranchs, restricting our ability to determine the extent to which ecomorphological theories may be applicable across chondrichthyan diversity. Our results show that, at least for some species, and at least for some aspects of morphology, theory originally developed to explain ontogenetic scaling in sharks also applies to batoids. Moreover, the apparent strong isometric correlation between disc width and total length in Rajiformes, Torpediniformes and Mobulidae suggests that even where only one measure is typically used in the existing

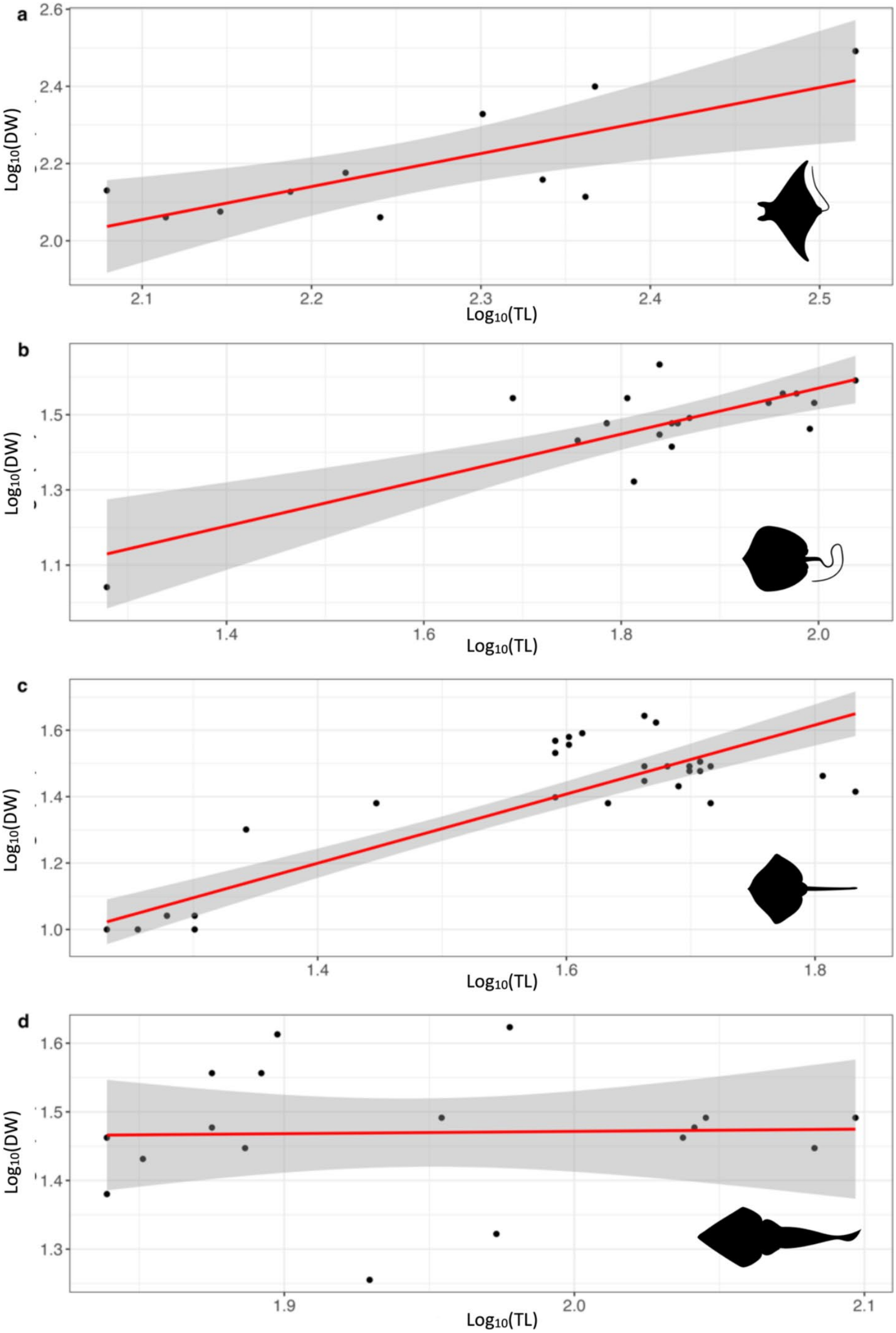

Fig. 5 scaling relationships between total length (TL) and disc width (DW) in male *M. tarapacana* (**a**), *F. margarita* (**b**), *R. parva* (**c**), and *R. irvinei* (**d**). Silhouettes are for illustrative purposes only and are not drawn to scale

Table 3 Scaling relationships between total length and disc width for male individuals only of each batoid species. Results that differ significantly from isometric expectations are indicated in bold

Species	*N*	Intercept (+/- SE)	Coefficient (+/- SE)	T	*P*	Adjusted R^2	F
M. tarapacana	9	0.2577 ± 0.544	0.8558 ± 0.2400	0.601	0.563	0.540	12.72
F. margarita	**16**	**0.3478 ± 0.216**	**0.6114 ± 0.117**	**3.331**	**0.004**	**0.609**	**27.47**
R. parva	33	-0.25782 ± 0.142	1.04095 ± 0.092	0.444	0.660	0.7883	127.6
R. irvinei	**15**	**1.40465 ± 0.53727**	**0.03342 ± 0.27573**	**3.505**	**0.003**	**-0.0656**	**0.015**

literature, both total length and disc width may be potentially valuable proxies for estimating overall body size/shape in both fossil specimens, and extant, partially processed batoids obtained from fisheries. These results are preliminary, and additional work testing this relationship across a far greater range of species is needed. Nevertheless, these findings provide important basic information regarding the morphometrics and ecomorphology of batoids that will serve as a foundation for this future work.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10682-024-10321-4.

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Author contributions JHG and IS conceived of the study, IS collected the data, JHG analysed the data, and all authors contributed to the writing and reviewing of the manuscript.

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Data availability All data associated with this study can be found in the online supplementary material associated with this article.

Declarations

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

Conflicts of interest/Competing interests The authors declare no conflicts of interest.

Ethics approval (include appropriate approvals or waivers): No ethics approval was required as all animals included in this study were dead, and taken as part of legal artisanal fisheries.

Consent to participate Not applicable.

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