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Biological traits as determinants in the macroecological patterns of distribution in loliginid squids

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Abstract

Macroecological studies have primarily focused on investigating the relationships between body size and geographic distribution on large scales, including regional, continental, and even global levels. While the majority of these studies have been conducted on terrestrial species, a limited number of studies have been carried out on aquatic species, and even fewer have considered the importance of phylogeny in the observed patterns. Cephalopods provide a good model for examining these macroecological patterns due to their large geographic and bathymetric ranges, wide range of body sizes, as well as diverse fin sizes and shapes. In this study, we assess the relationships between mantle length, fin size, and hatchling size with the geographic and bathymetric distribution of 30 squid species from the worldwide distributed family Loliginidae. To test a macroecological hypothesis, we evaluated the phylogenetic signal and correlated evolution to assess the role of biological traits in squid distribution, using a molecular phylogeny based on two mitochondrial and one nuclear genes. Biological traits (mantle length and fin size) exhibit high phylogenetic signals, while distribution demonstrates low signal. The correlation analyses revealed the existence of a relationship between adult mantle length and fin size with geographic and bathymetric distribution, but not with hatchling size. The geographic distribution of loliginid squids evolved in relation to mantle length, where larger squids with large fins (e.g. *Sepioteuthis*) have wide distributions, while small-finned species (e.g. *Pickfordia-teuthis*) have narrow distributions. This study paves the way for exploring similar relationships in other squid families or other marine swimming animals.

Keywords Squids · Macroecology · Phylogeny · Distribution · Dispersal capabilities · Loliginidae

Introduction

The geographic distribution of species is determined by ecological and evolutionary factors, as well as the dispersal abilities of each species, and environmental conditions (Brown

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et al. 1996). The locomotion mode aids species in migration and dispersal to colonize new habitats, thereby expanding their geographic ranges. Species that have evolved specialized anatomical structures for long-distance movement, such as wings or fins, exhibit wide geographic distributions (e.g. birds, bats, fishes) (Böhning-Gaese et al. 2006; Laube et al. 2013; Luo et al. 2019). Recently, Luo et al. (2019) demonstrated that bat species with larger wings have larger distribution ranges compared to those with smaller wings and that the size of geographic ranges was associated with wing aspect ratio. That study highlights the relationship between specialized anatomical structures and distributions, suggesting the significant role of dispersal capacity in shaping species' geographic distributions (Luo et al. 2019). In aquatic species, such as fishes and cephalopods, that utilize fins for locomotion, it is possible that the distribution patterns are going to be similar to those reported for birds and bats (Laube et al. 2013; Luo et al. 2019). On the other hand, in marine invertebrates, dispersal capabilities and consequently geographic distributions are influenced by larval size and movement capacities (Hansen 1980; Brown et al. 1996; Cowen and Sponaugle 2009; Villanueva et al. 2016; Ibáñez et al. 2018). Therefore, it is pertinent to investigate whether body size, fins, or larval dispersal influences the size of geographic ranges in marine invertebrates.

Cephalopods are exclusively marine animals that include nautilids, cuttlefishes, squids, and octopods, with approximately 860 species distributed across 50 families and 174 genera (Hoving et al. 2014; Luna et al. 2021). Some species reach large sizes as adults, enabling them to have wide geographic distributions spanning over 5000 km (Rosa et al. 2008a, b; Ibáñez et al. 2009, 2019; Rosa et al. 2012, 2019). They primarily inhabit the first 1000 m depth and have daily vertical migrations (Boyle and Rodhouse 2005). The combination of several characteristics, such as wide distribution, jet propulsion, high dispersal, and wide range of adult body size, makes cephalopods a good model for testing biogeographic hypotheses.

Since all cephalopods share funnel and jet propulsion, the distinct size and shape of fins could be determining factors in their movement capabilities (Clarke 1988). There are nine major fin shapes among squids, all of which contribute to fast swimming and orientation control (following Clarke 1988; Boyle and Rodhouse 2005). These fins are muscular hydrostats with an intramuscular network of crossed connective tissue fibres that provide support for fin movements (Johnsen and Kier 1993). Among pelagic squids, those belonging to the Loliginidae family display diverse fin morphologies, a wide amplitude of body sizes in both juveniles and adults, and high variability of geographic and bathymetric distribution (Anderson 2000a; Jereb et al. 2010). These traits make them an excellent study model to understand the factors that explain their distribution. Loliginidae contains

species which can reach a rather large size (at least 900 mm of mantle length, ML, in *Loligo forbesii*), along with dwarf species like *Pickfordiateuthis*, where females can mature up to 7.9 mm ML (Brakoniecki 1996). These benthopelagic squids have a pelagic paralarval stage, form schools, are active swimmers, and are chasing predators (Nesis 1980). Loliginid squids have elongated flapping fins that produce large-amplitude waves for economical, gentle swimming and hovering, as well as for controlling stability and aiding jet escape (Clarke 1988). By combining finning and jetting, cephalopods can generate different swimming gaits (Anderson and DeMont 2000; Stewart et al. 2010).

To understand the historical and ecological processes that influence the distributions of species, it is necessary to integrate comparative-quantitative biogeographic and phylogenetic studies (Brown et al. 1996; Hernández et al. 2013). In this study, we aim to test predictions of macroecology based on data about the distribution, fin characteristics (shape and size), and mantle length of both hatchling and adult loliginid squids worldwide. To achieve this, we collected data on distribution (latitudinal range, area, and depth) and biological traits (mantle length of young and adults and fin size) of loliginids. Additionally, with inferred the phylogenetic relationships of the loliginids to estimate the phylogenetic correlation between these traits. This study aims to test whether the geographic distribution can be predicted by dispersal capacity, inferred from mantle length and fin size, among loliginids within a phylogenetic comparative framework.

Materials and methods

Database

In this study, we included 30 species of loliginid squids from ten genera out of the 47 reported by Jereb et al. (2010). The data collected included squid mantle lengths (maximum mantle length, ML, mm, Fig. S1) as indicator of body size, hatchling size (ML), fin length (FL, mm, Fig. S1), and distribution (latitudinal range, bathymetric range, and area distribution). Fin shapes were classified as: rhomboid, round, or elliptic. In several loliginid species, males exhibit larger ML than females, while rarely females are larger (Jereb et al. 2010). This indicates different jet swimming capacities between genders. Additionally, some species, the maximum ML corresponds to only one gender. To explore the effect of mantle length gender on distribution, we conducted analyses separating the data based on gender when enough data were available. To avoid allometric effects, we transformed the fin length into fin length index (FLI, Roper and Voss 1983) (see supplementary material, Table S1). The distribution areas for all different species were estimated using maps from the literature (Jereb et al. 2010). To ensure accuracy,

we georeferenced these maps using the open-source GIS software QGIS 3.0.1 (QGIS Development Team 2018) with the plugin Georeferencer GDAL 3.1.9. This process assigned spatial information to each pixel in a map, relating it to a coordinate in geographic space. From the georeferenced maps, we recreated the distribution area as a polygon shapefile, from which we obtained its latitudinal range (in degrees) and area (km^2) with the plugin Calculate Geometry 0.3.2. We also recorded maximum depth of each species from the literature, to assess the bathymetric distribution range (m). This database was combined with a new molecular phylogeny reconstructed with data from GenBank (Table S2).

To assess the relationship between distributional data (latitudinal ranges, bathymetric range, and area distribution) and fin shape (rhomboid, round, and elliptic), we performed one-way ANOVA in R v4.1.2 core (R Development core team 2022), after log transformation of the data.

Phylogenetic analysis

Nucleotide sequences (16S, COI, and RHO) for each gene were separately aligned using Multiple Sequence Comparison by Log-Expectation (MUSCLE) with default parameters for gap insertion and gap extension (Edgar 2004), implemented in the MEGA X software (Kumar et al. 2018). The best-supported substitution model for each gene was identified prior to the phylogenetic analysis using jModelTest2 (Darriba et al. 2012) (Table S3). Once aligned, the sequences for each of the three genes were concatenated into a single partitioned matrix using Mesquite v3.10 (Maddison and Maddison 2016), which allowed for a separate substitution model to be used for each gene (Table S2).

We estimated phylogenies for the partitioned dataset using Bayesian Inference with MrBayes v3.2 software (Ronquist et al. 2012). Bayesian phylogenetic inference was performed using 10,000,000 generations of four heated Markov chain Monte Carlo (MCMC), sampling every 1,000 generations. We discarded the first 10% (1,000,000) of generations as burn-in, resulting in a total of 9,001 trees sampled from the posterior probability distribution. A majority consensus tree (50%) was computed from these 10,000 trees. We also evaluated convergence to the posterior distribution and mixing of the MCMC using Tracer v1.6 (Rambaut et al. 2014). Effective sample size (ESS) > 200 was accepted. The trees were rooted using *Spirula spirula* (Owen, 1836), *Ommastrephes bartramii* (Lesueur, 1821), and *Sthenoteuthis oualaniensis* (Lesson, 1830) as outgroups. Certain cryptic lineages (i.e. *Doryteuthis pleii*, *D. pealeii*, *Lolliguncula brevis*, and *Sepioteuthis lessoniana*) lacked morphometric and distribution data. Only the

lineages with the most data (and their respective distribution) were included in the phylogeny in order to avoid obscuring the results with cryptic species or genetic lineages (Okutani 1984, 2005; Segawa et al. 1993; Cheng et al. 2014).

For comparative purposes, all outgroup species (three tree tips, *S. spirula*, *O. bartramii*, and *S. oualaniensis*) were removed from the tree using the drop.tip function in "APE" package (Paradis et al. 2004), implemented in R v4.1.2 core (R Development Core Team 2022). The new phylogram was transformed into an ultrametric tree using the Grafen's (1989) method. To explore the association between the standardized database and the phylogeny, a heatmap was employed using the phylo.heatmap function in "Phytools" package (Revell 2012).

Phylogenetic signal

The ultrametric tree was used to estimate the phylogenetic signal of each trait, denoted as Pagel's λ (Pagel 1999). Lambda (λ) varies between 0 and 1, quantifying the amount of phylogenetic signal in the studied trait. A value of $\lambda = 0$ indicates that the trait distribution across species is independent of the phylogeny, while $\lambda = 1$ suggests that the distribution of trait values conforms to the expectations of the Brownian motion model (Pagel 1999). The analyses were conducted using the phylosig function, implemented in "Phytools". The likelihood value of λ estimated for each trait was compared to the likelihood value of λ equal to 0 through likelihood ratio test (LRT).

To determine whether fin shape exhibits a phylogenetic signal, we employed the "phylo.signal.disc" algorithm, comparing the number of transitions according to unrestrained parsimony against a null distribution obtained by randomizing the species data, effectively disrupting any underlying phylogenetic structure (Rezende and Diniz-Filho 2012). The null distribution was based on 1000 replicates and was implemented in R.

Correlated evolution

We used phylogenetic generalized least squares models (PGLS; Pagel 1999) to establish the existence of a linear relationship between ML (females, males, and hatchlings), FLI, and distribution data (latitudinal, bathymetric, and area). These models were performed using the corPagel function in the "APE" package in R. The correlation structure of PGLS was based on the assumption of Brownian motion model, multiplying the off-diagonal elements (the covariances) by λ. To compare all predictor variables, we calculate IC 95% for coefficients of all PGLS analyses.

Results

Biological data

The mantle length of the 30 loliginid species ranged from 22 mm in *Pickfordiateuthis pulchella* to 937 mm in *L. forbesii*, whereas fin length index ranged from 23 in *Alloteuthis africana* to 90 in *Sepioteuthis lessoniana* (Table S1). The geographic distribution ranged from 73,729 km² in *Lolliguncula argus* up to 28,000,000 km² in *S. lessoniana* (Table S1).

Among the distributional data, the only significant relationship was found between the distribution area compared with fin shape ($F_{2,27} = 5.158$, $P = 0.0127$); the species with elliptic shape had the larger distribution (see Fig. 1).

Phylogenetic signal

Both squids' mantle length (ML) (female and male) and fin length index (FLI) were highly structured across the phylogeny in the heatmap (Fig. 2), with both traits exhibiting a high significant phylogenetic signal ($\lambda > 0.75$, $P < 0.05$; Table 1). These results provide evidence of a concordance between loliginid phylogeny and both biological traits evaluated. All distribution data showed a low phylogenetic signal ($\lambda < 0.70$, $P > 0.5$; Table 1) and an absence of phylogenetic structure (Fig. 2).

Fin shape shows a higher correspondence with the phylogeny of loliginids (Fig. 3). The "phylo.signal.disc" algorithm for fin shape shows that five transitions were required to obtain the observed distribution along the loliginid phylogeny (Fig. 3). This result differed significantly ($P < 0.001$) from the median number of transitions (11; range 7–12) across the 1000 replicates employed to build the null distribution.

Correlated evolution

The largest loliginid squids have wider distribution, indicating a positive correlation with area distribution and bathymetric distribution (Table 2, Fig. 4). However, neither female nor male ML correlated with the latitudinal range ($\beta < 0.12$, Table 2, Fig. 4). The PGLS analysis showed a significant correlation between female and male ML with geographic distribution ($\beta > 0.75$, Table 2, Fig. 4). Similarly, FLI was positively and significantly correlated with area distribution and bathymetric range ($\beta > 1.0$, Table 2, Fig. 5), but not with latitudinal range ($\beta < 0.1$, Table 2, Fig. 5). Hatchling size did not show a correlation with the distribution data (Table 2, Fig. 5). Among all predictor traits (body size, hatchling size, and fin length), the best predictor of geographic and bathymetric distribution of loliginid squids was FLI ($\beta = 1.4$–2.4, Table 2, Fig. 6). Finally, the box-and-whisker plot does not show clear differences between female and male coefficients for all PGLS analyses.
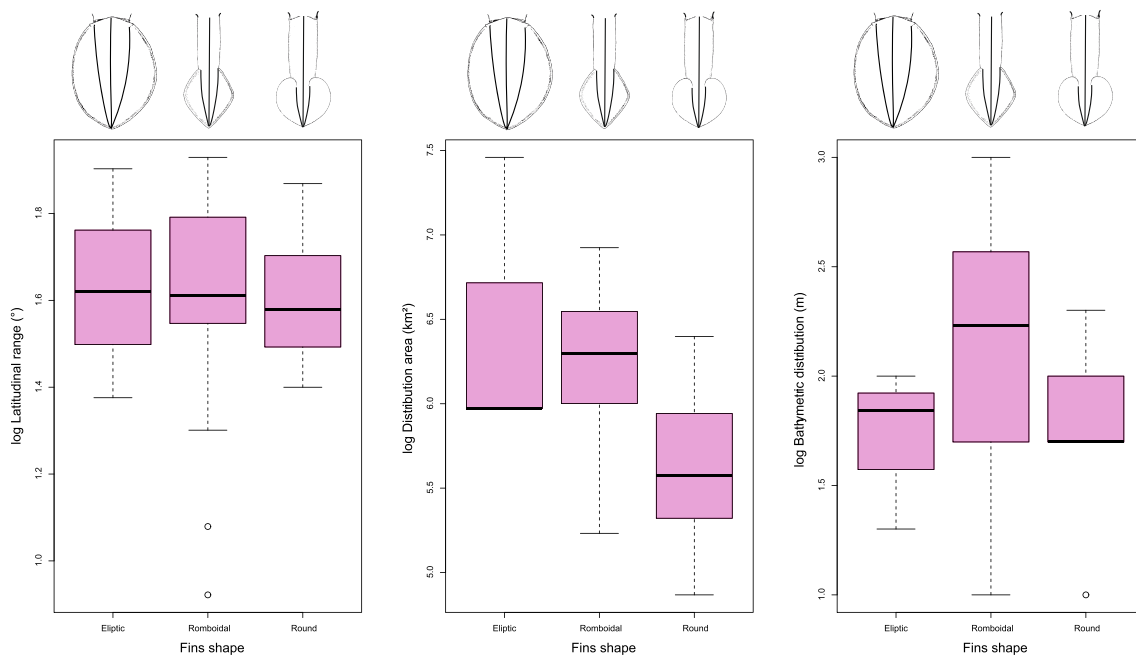

Fig. 1 Box plots showing the distribution data by fin shape. Boxes represent percentiles of 25% and 75%, and the bar represents the 95% confidence interval (CI)

Fig. 2 Phylogenetic heatmap tree of loliginid squid biological and distributional traits. The scale bars are in standard deviation (SD) units for each column of data
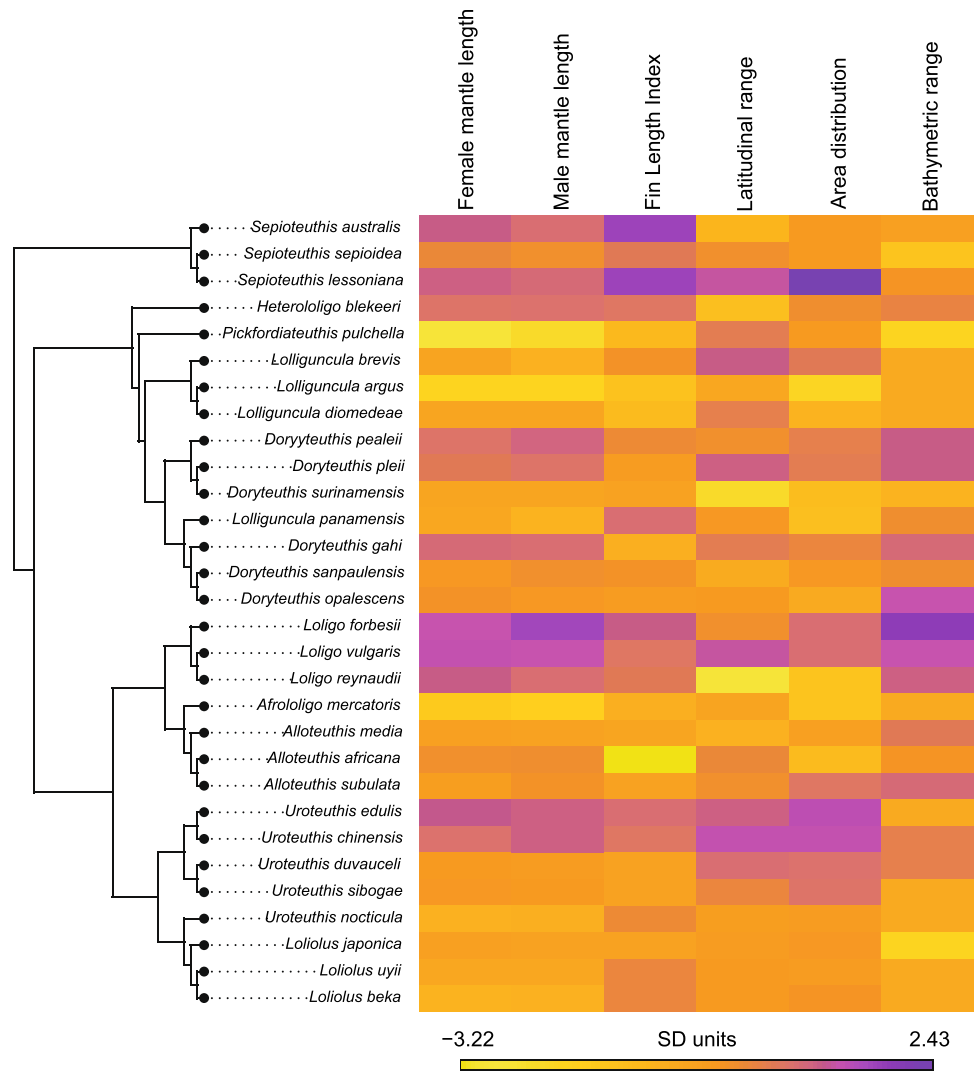

Table 1 Phylogenetic signal of each trait obtained with univariate analyses

	Lambda (λ)	logLik λ	logLik $\lambda = 0$	*P* value
FML	0.949	− 186.192	− 188.992	0.018
MML	0.919	− 202.003	− 202.604	0.027
FLI	0.761	− 118.927	− 122.037	0.013
Latitude	0.000	− 132.209	− 132.208	1.000
Area	0.090	− 506.614	− 506.675	0.726
Depth	0.632	− 201.941	− 202.786	0.194

Discussion

Geographic range size, which refers to the extent of a species' occurrence, is a fundamental biogeographic variable influenced by several intrinsic and extrinsic factors (Brown et al. 1996; Gaston 2003). In the case of loliginid species,
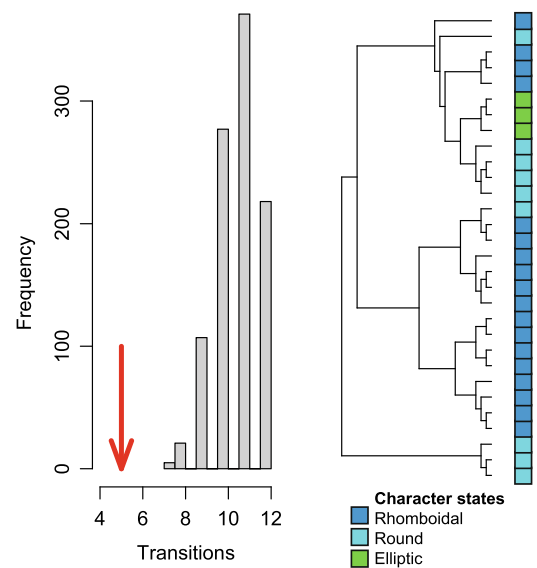

Fig. 3 Phylogenetic signal of fin shape of loliginid squid

Table 2 Parameters of the relationship among mantle length (ML), fins length index (FLI), and geographic distribution of loliginid squids obtained by phylogenetic generalized least squares (PGLS) analyses

Latitudinal range	Female ML	Male ML	FLI	Hatchling ML
λ	0.1565	0.1752	0.1663	−0.0019
logLik	−0.6421	−0.5745	0.2193	−1.8005
α	1.3922	1.3500	1.7741	1.6637
β	0.0898	0.1075	−0.1070	−0.1278
SE	0.1293	0.1058	0.3773	0.2594
t value	0.6942	1.0162	−0.2834	−0.4925
P value	0.4933	0.3182	0.7789	0.6283
Distribution area	Female ML	Male ML	FLI	Hatchling ML
λ	0.1570	0.1979	−0.0034	−0.1681
logLik	−21.6914	−20.4387	−21.8995	−14.3162
α	3.9798	4.1231	1.8342	5.8792
β	0.9272	0.8501	2.4319	0.6993
SE	0.2742	0.2150	0.7994	0.5320
t value	3.3812	3.9542	3.0421	1.3146
P value	0.0021	0.0005	0.0051	0.2052
Bathymetric range	Female ML	Male ML	FLI	Hatchling ML
λ	0.4104	0.3379	0.6992	0.7270
logLik	−14.5215	−14.2278	−18.2750	−10.0345
α	0.0765	0.3263	−0.4122	2.2618
β	0.8764	0.7532	1.4090	−0.2209
SE	0.2110	0.1722	0.7396	0.3752
t value	4.1529	4.3727	1.9052	−0.5888
P value	0.0003	0.0002	0.0671	0.5633

we observed that larger species with larger fin sizes have broader bathymetric and geographic distribution, akin to the positive correlation between wings and distribution observed in birds and bats (Böhning-Gaese et al. 2006; Laube et al. 2013; Luo et al. 2019). This macroecological relationship suggests exploring these patterns in other squid families or marine swimming animals (e.g. fishes) to understand whether the geographic range size is related to these and other biological traits.

The geographic distribution, encompassing area and latitudinal and bathymetric range, does not exhibit a significant phylogenetic signal throughout the family. This contradicts the statements made by other authors (Brakoniecki 1986; Anderson 2000a, b; Ulloa et al. 2017), who posited that geographically close species share common ancestors. However,

our data are quantitative (i.e. km^2), not qualitative (i.e. biogeographic provinces), and thus do not exhibit significant phylogenetic signal. In contrast, biological traits (i.e. body size and fins) have a strong phylogenetic signal, as suggested by other studies on cephalopods (Ibáñez et al. 2018; 2021; Anderson and Marian 2020).

The geographic distribution of loliginid squids is suggested to be influenced by their environment and ecology (Sales et al. 2013, 2017; Costa et al. 2021). One crucial factor is their dispersion capacity. For certain American Loliginid species from the *Doryteuthis* and *Lolliguncula* genera, the Amazon plume Barrier (Floeter et al. 2008) does not impede the dispersion of *D. pleii*, *D. pealeii*, and *L. brevis* above the major influence area of the plume (between Pará and Amapá states, and North Coast of Brazil, Muller-Karger et al. 1988; Hoorn et al. 2010), despite the significant reduction in salinity. However, low-salinity environments can act as barriers for both adults and paralarvae, resulting in high mortality (Hanlon and Messenger 1996; Hanlon 1998; Boyle and Rodhouse 2005). Nevertheless, the considerable capacity of dispersion of loliginid squids is evidenced by that these species do in fact disperse above the plume area of influences (Boyle and Rodhouse 2005; Jereb et al. 2010).

Body size and distribution

Our results show that loliginid squids with larger body size, both females and males, exhibit a larger geographic distribution, while smaller species have a restricted distribution, similar to some marine fishes (Hernández et al. 2013). However, the swimming capacity of squids differs that of fishes. For millions of years, cephalopods roamed the world's oceans as jet-propelled masters of the pelagic world, until fishes, using highly efficient undulatory locomotion, displaced them from many nektonic habitats (Hoar et al. 1991). According to Nesis (1980), the evolution of squids, such as Loliginidae, has been strongly influenced by competition with fishes. In fact, their biology, distribution, and geographic variation are determined by direct competition between species that occupy different ecologic habitats (depth and thermal preferences) and exhibit inverse circadian activity levels (Martins and Juanicó 2018). Indeed, the directional jet propulsion of the cephalopods provides better acceleration and manoeuvrability than many fishes (Foyle and O'Dor 1988). Combined with lift production by the fins, squids may have more dynamic lift capabilities (Hoar et al. 1991). In this study, the positive relationship between mantle length, fin length, bathymetric range, latitudinal range, and distribution area suggests that dispersal capacity plays a role in shaping species' geographic distributions. When there are no geographic or ecological barriers preventing it, larger
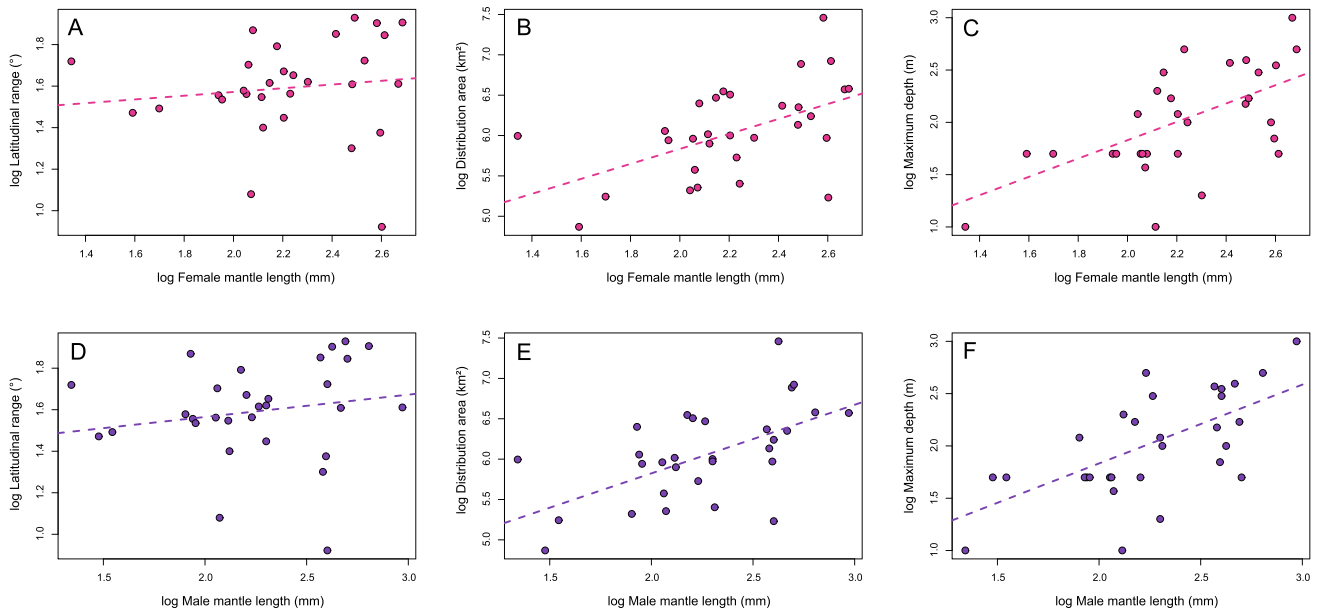
Fig. 4 Plots illustrating the relationships between female and male mantle length and distributional traits of loliginid squids, where **A** female mantle length/latitudinal distribution, **B** female mantle length/ geographic distribution, **C** female mantle length/bathymetric distri-bution, **D** male mantle length/latitudinal distribution, **E** male mantle length/geographic distribution, and **F** male mantle length/bathymetric distribution. Dashed lines represent regressions from PGLS

squid will have greater dispersal capacity, enabling them to reach a wider distribution range.

The geographic distribution of loliginids appears to have evolved in relation to body size. Larger squids (*Sepioteuthis*) have wide distributions, while smaller species (*Pickfordiateuthis, Afrololigo*) have narrow distributions (Fig. 2). Previous studies in vertebrates have detected a positive relationship between geographic range size and body size
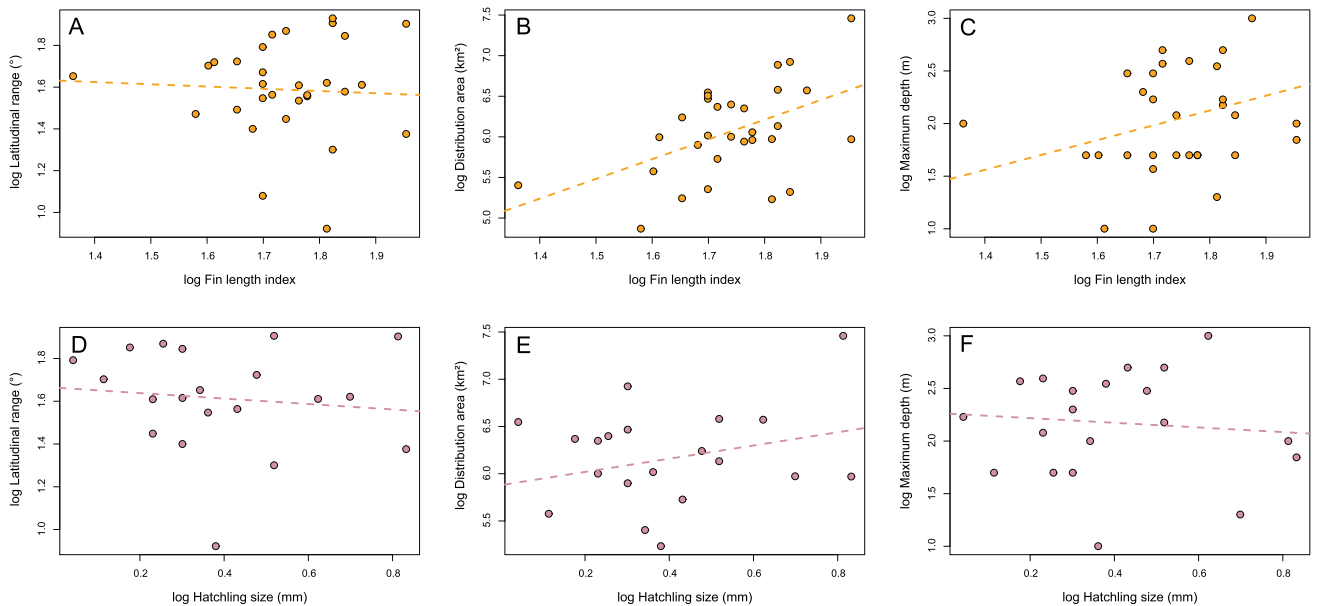

Fig. 5 Plots depicting the relationships between biological and distributional traits of loliginid squids, where **A** fin length index/latitudinal distribution, **B** fin length index/geographic distribution, **C** fin length index/bathymetric distribution, **D** hatchling mantle length/latitudinal distribution, **E** hatchling mantle length/geographic distribution, and **F** hatchling mantle length/bathymetric distribution. Dashed lines represent regressions from PGLS
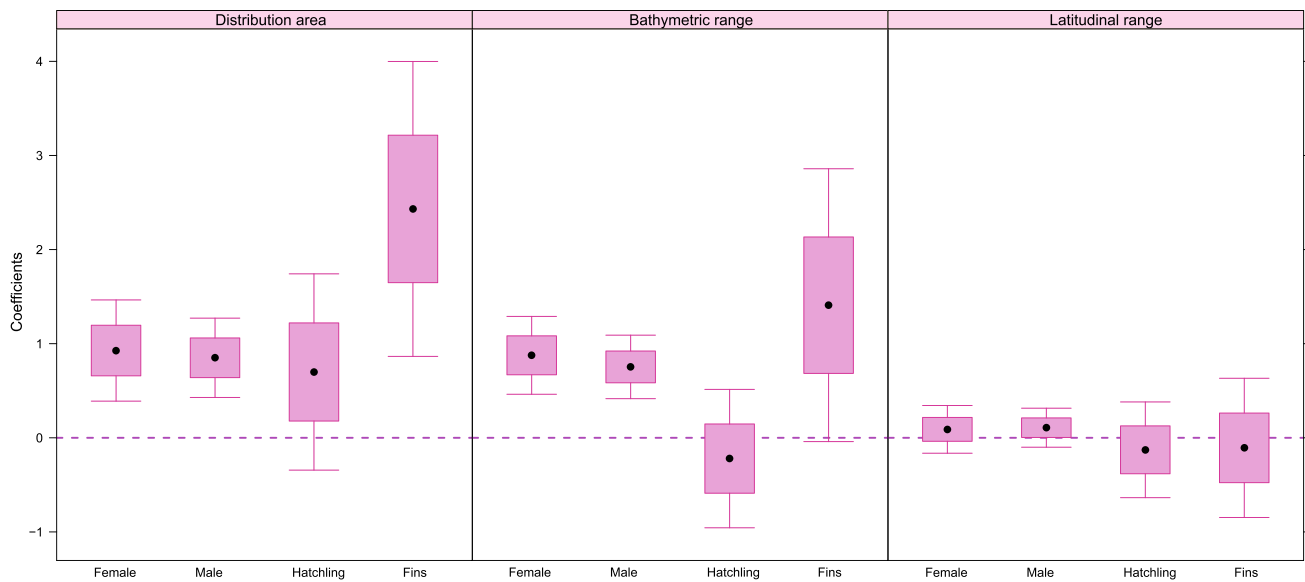
Fig. 6 Box-and-whisker plots showing the PGLS coefficients of all phylogenetic regressions. The boxes represent the percentiles of 25% and 75%, and the bar represents the 95% confidence interval (CI)

(Diniz-Filho and Tôrres 2002; Hernández et al. 2013), which is consistent with the relationships between mantle length and geographic distribution in our results (Fig. 4). However, the existence of significant variation in the sizes of geographic ranges among small species is a common pattern in macroecology (Brown 1995). Species falling below to regression line (ML vs distribution) have a smaller spatial distribution than predicted by its body size, for instance, *L. argus*, a coastal species characterized by its small size at maturity (Jereb and Roper 2010), which would decrease its potential final size. This species reaches the smallest area of all the studied loliginid species (73,729 km^2). A similar case occurs in the small species that inhabits sandy-mud bottoms *Afrololigo mercatoris*, which shares many morphological traits with *Lolliguncula* (Jereb et al. 2010), such as the small size.

Size and shape have important implications for the hydrodynamics of marine organisms (DeMont and Hokkanen 1992). The absence of shared common ancestors along geographically close species may be determined by the biology and dispersal ability of each species. Indeed, the high mobility of adult loliginids (Boyle and Rodhouse 2005) makes their dispersal more widespread. A notable case is that of the three neritic species of the genus *Loligo*, which have a high dispersal ability, and an evident difference between the maximum ML of their males, which could be one of the reasons for habitat choice (*L. forbesii*, *L. vulgaris,* and *L. reynaudii*; Jereb et al. 2010; Iwata et al. 2018). Similarly, in adults of *A. africana* and *Uroteuthis bartschi* (maximum ML of 200 mm in males, 150 mm in females; Voss 1963; Jereb et al. 2010), there is a remarkable sexual dimorphism,

where males display the characteristic extremely long and spike-like tail (73% of the dorsal ML in *A. Africana* adults) as secondary sexual trait. However, our results did not reveal a strong difference in distribution related to ML of females and males. In this line, both genders have the same dispersal capacity and sexual dimorphism could be related to other factors (e.g. growth, reproduction).

Fins shape/length and distribution

Fin length and shape exhibit a highly significant phylogenetic signal, demonstrating the existing concordance between the fin size and shape and loliginid phylogeny. Fins shape undergoes changes during ontogenetic growth, with hatching squid having fins proportionally smaller than those of adults. This change in relative size may also reflect a shift in the use of the fins, similar to the different usages of the variously shaped adult fins (Hoar et al. 1991). The shape of the lateral fins of cephalopods varies in accordance with the animal's size and lifestyle (Packard 1972), with hydrodynamic constraints being primary determinant of fin shape (Daniel 1988). For species such as from the genus *Uroteuthis*, fins play an efficient role in maintaining position in the water column. As growth occurs, and the animal transitions from a viscosity-dominant to an inertia-dominant system, the development of the fin structure becomes crucial, with shape further influencing friction and pressure drag on animals during movement (Moltschaniwskyj 1995).

Fin size emerges as the most important biological trait for predicting the distribution of loliginid squids (Fig. 6), with species possessing the largest elliptical fins (i.e.

Sepioteuthis) exhibiting wider distributions. *Sepioteuthis lessoniana,* widely distributed throughout the Indo-Pacific and Mediterranean regions, is the species with the broadest range of distribution among these squids. The genus features very large and distinctive fins, broadly oval in outline and with a fin length comprising over 90% up to nearly 100% of ML (Jereb et al. 2010), making them markedly different from other loliginids. In contrast, *Sepioteuthis australis,* distributed in the southwestern Pacific Ocean, is distinguished from *S. lessoniana* by the angular lateral margins of its fins, although not by the fin length (Jereb et al. 2010). The distant geographic distribution of both species may explain this contrasting phylogenetic footprint. On the other hand, the loliginids *A. africana* and *L. argus* have the smallest FLI and limited distribution. Among the medium-sized, continental shelf species, *Uroteuthis* (*P.*) *edulis* exhibits a broad fin (70% ML in length, 60% ML in width), as does its congener *Uroteuthis* (*P.*) *chinensis* with a fin spreading to two-thirds of the ML. However, both *Uroteuthis* have a less extensive range of distribution than it would be expected based solely on their fin size.

Another important factor affecting the dispersal capacity of the loliginids is the speed they can achieve in swimming and their manoeuvrability, combining finning and jetting to generate different swimming gaits (Anderson and DeMont 2000; Stewart et al. 2010). For instance, there are differences between the locomotive repertoire and the high degree of manoeuvrability enabled by fin propulsion of *Loliguncula brevis* (Bartol et al. 2001) than the extensive use of the fins for swimming of the ommastrephid *Illex illecebrosus* (Harrop et al. 2014). In the first species, its swimming gaits could help them achieve a distributional range similar to that of larger loliginids. The high diel vertical migration behavioural flexibility expressed by *L. forbesii* could be very advantageous in terms of energy conservation, prey capture, and predator avoidance (Cones et al. 2022), leading to greater evolutionary success and, consequently, a larger dispersal capacity than expected for its size.

Hatchling size and distribution

Marine mollusc species lacking a planktonic larval phase in their life cycle tend to have smaller size ranges compared to species with more readily dispersed planktotrophic larvae (Brown et al. 1996; Villanueva et al. 2016; Ibáñez et al. 2018). In fact, some Neogastropoda snails exhibit wide distributions, extended gene flow, and resistance to isolation, resulting in greater species longevity for species with planktonic larvae (Hansen 1980). Loliginids, on the other hand, have a pelagic paralarval stage during which they spend two to three months in the plankton (Garcia-Mayoral et al. 2020). During this time, they disperse but remain on the continental shelf by controlling their vertical position

(Roura et al. 2016, 2019). Consequently, this group tends to have large size ranges, leading to extensive geographic distribution (Villanueva et al. 2016). Some squids exhibit very high dispersal rates, due to lengthy planktonic paralarval stages and highly migratory adult stages, leading some authors to predict panmixia (genetic homogeneity) of squid populations across large geographic areas (e.g. Shaw et al. 2010). Nonetheless, many loliginid squids show structured population at large scales (Brierley et al. 1995; Shaw et al. 1999; Herke and Foltz 2002; Aoki et al. 2008; Ibáñez et al. 2012). This pattern is associated with reduced paralarval dispersion, since eggs are deposited on the seabed or attached on sessile organisms (e.g. kelps, corals), which promotes structure between populations (Carrasco et al. 2021).

Despite all this, our results show that species of loliginid squids (both females and males) falling above the regression line (ML vs distribution, Fig. 4) have larger distribution ranges than predicted by their body size. This pattern could be associated with paralarval dispersion, but our results do not support the idea that paralarvae dispersion explains the wide distribution of some species, as our analyses did not find a correlation between hatchling size and distribution data (Fig. 5). This might indicate a reduction in distribution, or it could suggest that our knowledge of their distribution is still lacking.

In this comparative study, we evaluated the potential effects of body size (young and adults) and fins (shape and size) of squids as predictors of their distribution using a phylogenetic approach. This approach has been scarcely used in macroecological studies on marine animals, particularly in the assessment of phylogenetic signal on geographic distribution (i.e. Hernández et al. 2013; Ulloa et al. 2017; Ibáñez et al. 2018). In this sense, our research is among the first studies correctly address trait comparisons for marine animals, suggesting that further research should incorporate this approach in macroecological studies. New approaches to the knowledge of the distributional range of mobile species, such as the bio-logging tags (Flaspohler et al. 2019; Cones et al. 2022), or eDNA could help in accurate assessments of the real extent of the species, as well as their biological activity and behavioural patterns.

Data availability All data of this article is in supplementary files.

Declarations

Conflict of interest The authors declare that they have no conflict of interest and also no financial interests.

Ethical approval Ethical review and approval were not required for this study because this work does not contain any experimental studies with live animals. Biological, distributional data, as well as sequences, were taken from open sources (i.e. GenBank, FAO books). This study did not need ethical approval since it was based on literature review and published information.

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