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A morphospace for the Eocene fish assemblage of Bolca, Italy: a window into the diversification and ecological rise to dominance of modern tropical marine fishes

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KEY WORDS - Geometric morphometrics, morphospace occupation, Eocene, Konservat-Lagerstätte, teleost fishes.

ABSTRACT - The celebrated Eocene fishes of Bolca, northeastern Italy, provide one of the earliest evidence of a modern tropical shallow marine fish assemblage, in the aftermath of the end-Cretaceous extinction. This fish assemblage has been traditionally interpreted as closely linked to a coral reef system based on a certain similarity in taxonomic composition with modern ecosystems. In this study, we use geometric morphometrics to compare the patterns of morphospace occupation and morphological variation between Eocene and extant tropical shallow water fish assemblages. Morphospace analysis revealed that there are not significant differences in morphospace occupation, and the Eocene fish assemblage shows a greater frequency of deep-bodied morphotypes and a higher morphological disparity compared to the extant tropical marine shallow-water assemblages. Because of the highly reduced reef-building potential of early Eocene coral communities and the extremely scarce evidence of corals in the Bolca area, the broad morphospace occupation and the high morphological richness observed for the Bolca assemblage suggest that an Eocene tropical non-coral reef setting shows higher, or at least similar, morphological diversity than modern coral reef-associated fish assemblages. Therefore, our paleontological evidence suggests that coral reefs may have played a secondary role in shaping the morphological richness of these fossil and extant tropical marine fish assemblages, and are consistent with the hypothesis of the rapid niche-filling and early saturation of the teleost morphospace after the end-Cretaceous extinction.

RIASSUNTO - [Analisi del morfospazio dell'ittiofauna eocenica di Bolca, Italia: Uno sguardo all'interno della diversificazione e dell'ascesa ecologica delle associazioni ittiche tropicali moderne] - L'ittiofauna eocenica di Bolca costituisce una delle più antiche evidenze di associazioni ittiche neritiche tropicali di tipo moderno, originatesi a seguito dell'estinzione tra Cretaceo e Paleogene. Tale associazione ittica è stata tradizionalmente interpretata come associata ad un sistema recifale sulla base di una apparente somiglianza nella composizione tassonomica con gli attuali ecosistemi caratterizzati dalla presenza di barriere coralline. In questo studio, attraverso l'uso della morfometria geometrica, vengono comparati i patterns di occupazione del morfospazio e di variazione morfologica tra le associazioni ittiche neritiche tropicali eoceniche e attuali. L'analisi del morfospazio non ha rivelato differenze significative relativamente all'occupazione del morfospazio, sebbene l'associazione ittica di Bolca mostri una cospicua frequenza di morfotipi dal corpo elevato e una maggiore disparità morfologica rispetto alle attuali associazioni ittiche neritiche tropicali. Considerati il ridotto potenziale di biocostruzione delle comunità coralline dell'Eocene inferiore e la scarsa evidenza di coralli nell'area di Bolca, l'estesa occupazione del morfospazio e l'elevata ricchezza morfologica dell'associazione ittica di Bolca sembrano suggerire che ambienti tropicali neritici eocenici privi di sistemi corallini potevano essere caratterizzati da una diversità morfologica simile o maggiore di quella osservata per le associazioni ittiche neritiche tropicali odierne associate a sistemi recifali. Pertanto, le evidenze paleontologiche sembrano indicare che le barriere coralline possano aver giocato un ruolo secondario nel plasmare la ricchezza morfologica delle comunità ittiche marine tropicali. Tali evidenze, inoltre, appaiono in accordo con l'ipotesi di una rapida occupazione delle nicchie e una precoce saturazione del morfospazio dei teleostei a seguito dell'estinzione di fine Cretaceo.

INTRODUCTION

The Eocene (late Ypresian, ca. 50 Ma; Papazzoni & Trevisani, 2006) Bolca Konservat-Lagerstätte, northern Italy, has provided one of the most complete and well-preserved fossil marine fish assemblages. The fossils of these deposits document a tropical marine shallow-water ecosystem in which fish taxa are in many cases comparable to those alive today that are associated with modern coral reefs (Choat & Bellwood, 1991; Bellwood & Wainwright, 2002). Consequently, the Bolca assemblage has been traditionally regarded as the oldest evidence of a coral reef community (Blot, 1969, 1980; Sorbini, 1972; Bellwood, 1996). It is a common idea that the taxonomic and morphological richness of the reef fish assemblages, including that of Bolca,

is related to the presence of coral reef systems acting as drivers promoting fish diversity (e.g., Bellwood et al., 2005; Rüber & Zardoya, 2005; Alfaro et al., 2007; Hoeksema, 2007; Cowman & Bellwood, 2011; Frédérick et al., 2013; Sorenson et al., 2014). Studies devoted to elucidate the evolutionary dynamics of teleosts suggest that the morphological diversification of modern reef fish lineages is the result of the evolutionary radiation in the aftermath of the end-Cretaceous mass extinction that took place to replace the ecological roles left unoccupied by the extinction victims (Friedman, 2009, 2010). Moreover, several studies (Bellwood & Wainwright, 2002; Price et al., 2014, 2015) hypothesized that modern fishes living on coral reefs originated from non-reef lineages which colonized reefs during their evolutionary history. Bolca dates back about 16 Ma after the end-Cretaceous

extinction, corresponding to a period of maximum morphological diversification of the major fish lineages (Friedman, 2010; Near et al., 2013) and coincident to the early Paleogene crisis of coral reefs (e.g., Zamagni et al., 2012). In this context, the comparison of morphospace occupation and morphological diversity (i.e., disparity; Foote, 1992) between Eocene and modern tropical shallow marine fish assemblages could provide paleontological evidence to support the hypothesis of the rapid saturation of the ecological niche (niche-filling scenario, see Friedman, 2009, 2010; Price et al., 2014) as the driving force of the morphological richness of the Paleogene fish communities.

Analysis of fish body shape is a powerful tool to explore the patterns of morphospace occupation in complex ecosystems (e.g., Walker, 2010; Farré et al., 2013). In this study, we applied geometric morphometrics (Bookstein, 1991; Rohlf & Marcus, 2003; Zelditch et al., 2004) in order to decipher these patterns in Eocene and extant marine shallow-water fish assemblages. The main goal of this study is to compare the overall morphospace of the Bolca fish assemblage with that of modern reef-associated communities in term of body-plan organization. Specific aims are: 1) to decipher similarities and differences in the morphospace occupation, both in terms of overlap and distribution of the taxa in the morphospace, and 2) to compare the morphological diversity between Eocene and Recent tropical shallow marine ecosystems. These comparisons may provide new insights useful to understand evolutionary trends in overall morphospace occupation and to interpret the morphospace of modern fish assemblages which are supported by coral reef systems.

MATERIALS AND METHODS

Taxon sampling

In order to compare fossil and Recent fish assemblages, the genus was used as the standard unit because the concept of fossil species does not correspond to the biological one (Bock, 2004) and the genus is considered as a reliable taxonomic rank to analyze biodiversity (Forey et al., 2004). Moreover, since genera have more complete records than do species, morphospace analysis was performed at the genus level using a single species as representative of the morphology of each genus (see Cavin et al., 2007).

The genus-level database contains 1101 teleost genera, 918 extant and 183 fossil (Tabs S1 and S2). The images of extant fishes were obtained from the online picture repository of FishBase (<http://www.fishbase.org>; Froese & Pauly, 2014), as well from the photographs taken by Dr. John E. Randall at the Bishop Museum (<http://pbs.bishopmuseum.org/images/JER/images.asp>). Although the majority of the fossil specimens was examined and photographed in numerous collections, some of these were taken from published photographs or specimen drawings. The Eocene teleost assemblage of Bolca (183 taxa; see Carnevale et al., 2014) was compared to the shallow-water teleost communities of four large ecosystems pertaining to the Indo-Pacific and Western Atlantic realms (data from <http://www.fishbase.org>), namely the Great Barrier

Reef (513 genera), Red Sea (475 genera), East Brazil Shelf (292 genera) and Caribbean Sea (394 genera). The Recent ecosystems were chosen because they represent some of the possible modern analogues of the marine paleobiotopes in which the Eocene fossils of Bolca were accumulated (Bellwood, 1996; Landini & Sorbini, 1996; Papazzoni & Trevisani, 2006).

Geometric morphometrics protocols

The body shape and the structure of fish assemblages were studied analyzing their respective morphospaces through landmark-based geometric morphometric method (Zelditch et al., 2004). A total of 13 landmarks and 26 semilandmarks were digitized using the software package TPSdig 2.05 (Rohlf, 2005). Landmarks were selected on the basis of their possible ecological or functional role following the scheme applied in some studies about shape variation in modern or extinct fishes (Fig. S1). The landmark coordinates were translated, rotated and scaled at unit centroid size by applying a Generalized Procrustes Analysis (GPA) to minimize the variation caused by size, orientation, location and rotation (Zelditch et al., 2004). The GPA was performed using the TPSrelw software package (Rohlf, 2003). The Procrustes coordinates represent new shape variables, which are decomposed into Uniform and Partial Warp components. Subsequently, a principal component analysis (PCA) was performed on Procrustes coordinates to obtain the Relative Warp (RW). RWs are vectors describing the maximum variation of specimen shape compared to the consensus configuration (mean shape). The two-dimensional morphospace of each assemblage was defined using the area inside the convex hull (i.e., minimum convex polygon; Cornwell et al., 2006) built on the first four RWs explaining over 5% of the variance (Zelditch et al., 2004; Recasens et al., 2006). Changes in shape along these axes were visualized through deformation grid plots (Fig. S2). Since most of the fossil taxa are known only from one specimen and the development stage may be uncertain, we analyzed the effect of body size on morphospace occupation. A regression was performed between the shape and the centroid size, and an ANOVA was applied to verify the effect of body size on the shape (Fig. S3; Tab. S3).

Patterns of morphospace occupation and morphological disparity

To assess significant differences in morphospace occupation among fish assemblages we used two non-parametric tests. The multivariate analysis of variance (PERMANOVA; Anderson, 2001) was applied to detect significant differences in the group centroid positions. A PCA was applied to the average values of the Procrustes coordinates of all the taxa in each fish assemblage in order to have a visual image of the landmark configuration at the centroid of each ecosystem. The analysis of similarities (ANOSIM; Clarke, 1993) was employed to test for significant overlap between convex hulls. Statistical significance was calculated along all RWs with 9,999 random permutations. Euclidean distances were chosen as distance measure and the Bonferroni correction was applied for both tests.

In order to compare patterns of morphospace occupation between the Bolca and extant fish assemblages,

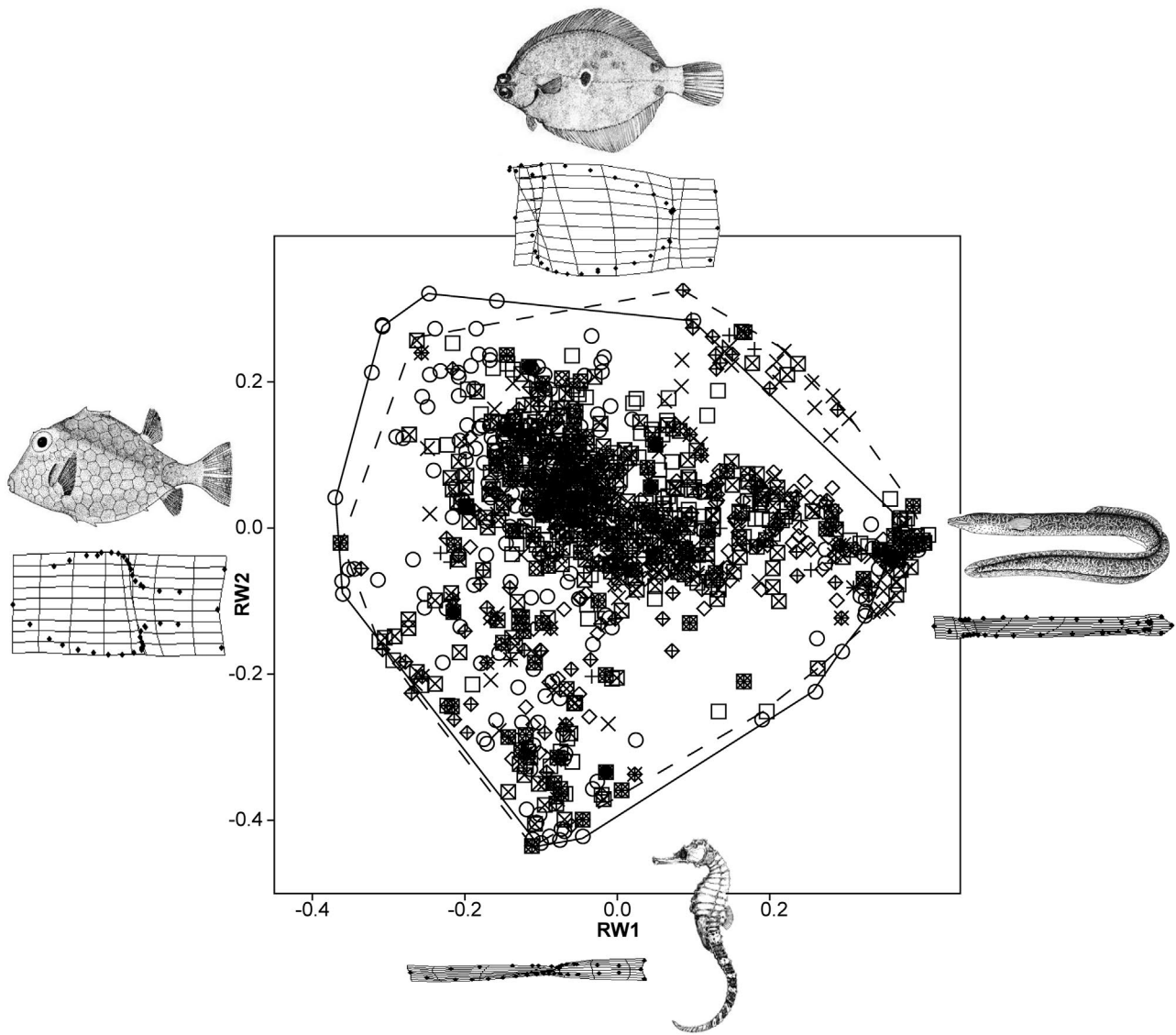


Fig. 1 - Overlapping convex hulls of all fish assemblages plotted on the first two RW axes explaining the greatest variance (66.7%). The full line represents the convex hull of the Bolca fish assemblage; the dashed line encloses all modern fishes. The illustrated taxa are some representatives of the extreme shapes that lie along extreme values of each axis, also visualized through deformation grids. Bolca = circle; Great Barrier Reef = square; Red Sea = x-cross; Caribbean Sea = diamond; East Brazil Shelf = cross.

we calculated the area and the distribution of data in the morphospace (patterning) and the morphological disparity (e.g., Foote, 1993, 1994; Villéger et al., 2011; Tuset et al., 2014).

Nearest neighbour analysis (Davis, 1986) was made to interpret clustering or overdispersion of taxa, also providing data on area, density and other basic statistic values of the patterning. Although the area of convex hulls is often used as a measure of functional richness (e.g., Villéger et al., 2008; Werdelin & Lewis, 2013), we simply interpret it as a pure value of the width of the morphospace because it is not clear if a space describing shape variation also describes functional changes in fish assemblages (Wainwright et al., 2005). The patterning was also visualized through Kernel-density plots, which provide a direct visual image of taxon distribution showing areas where taxa are close together in the morphospace and

gaps in which taxa are less densely distributed or absent (Werdelin & Lewis, 2013; Tuset et al., 2014).

Morphological disparity is defined as the measure of morphological variability (Foote, 1992, 1993) and it was calculated as the sum of variances, which is insensitive to the sample size (Ciampaglio et al., 2001). A 95% confidence interval was computed adopting a bootstrap procedure (999 repetitions) to take into account the uncertainty of the mean shape calculated in the hyperspherical morphospace, and to eliminate the effect of sample size (Zelditch et al., 2003, 2004).

All graphics, RW analysis and statistics were performed using the software packages TPSrelw 1.36 (Rohlf, 2003), PAST 2.17c (Hammer et al., 2001), and R 3.0.2 (R Core Team, 2015). Additional details on dataset list and geometric morphometrics are discussed in the Supplementary online material.

RESULTS

Relative warp analysis

After GPA, the RW analysis is summarized by 74 RW axes, with the first four together accounting for over 86% of the total morphological variability. The first two RWs (66.7% of overall variance) describe the correlation between elongation of fish and median-fin base length (Fig. 1). Positive scores of RW1 (39.4% of variance) indicate slender and elongate body shapes with long median fins (e.g., Anguilliformes and Ophidiiformes); conversely, negative values are related to deep-bodied fishes with short median fins (e.g., Tetraodontiformes). Positive scores of RW2 (27.3% of total variance) indicate deep-bodied fish taxa with long median fins (e.g., Pleuronectiformes);

conversely, negative values define slender bodies and short dorsal and anal fins (e.g., Syngnathiformes). RW3 and RW4 (19.6% of overall variance) explain mostly the shape and size of the caudal peduncle with respect to the rest of the body (Fig. 2). In particular, the RW3 (12.7% of variance) describes the caudal peduncle length while the RW4 (6.9% of total variance) explains the preanal distance.

Patterns of morphospace occupation and morphological disparity

The quantitative occupation patterns are supported by the results of non-parametric tests calculated along all RW axes (Tabs S4 and S5). The PERMANOVA rejects the null hypothesis of equal group centroids between the Bolca assemblage and those of other ecosystems ($p = 0.001$).

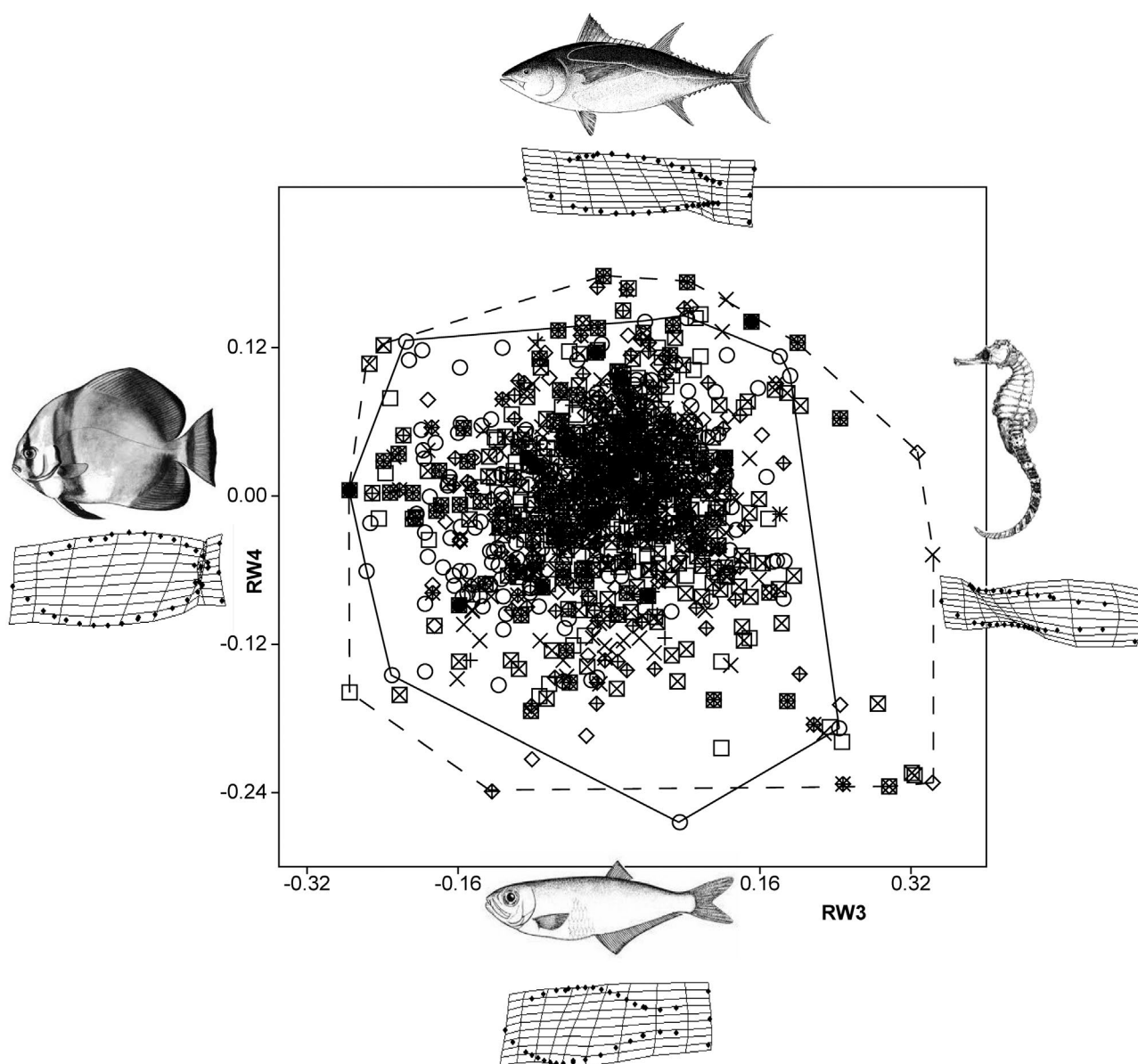


Fig. 2 - Overlapping convex hulls of all fish assemblages plotted on the third and fourth RW axes explaining 20.4% of the variance. The full line represents the convex hull of the Bolca fish assemblage; the dashed line encloses all modern fishes. The illustrated taxa are some representatives of the extreme shapes that lie along extreme values of each axis, also visualized through deformation grids. Bolca = circle; Great Barrier Reef = square; Red Sea = x-cross; Caribbean Sea = diamond; East Brazil Shelf = cross.

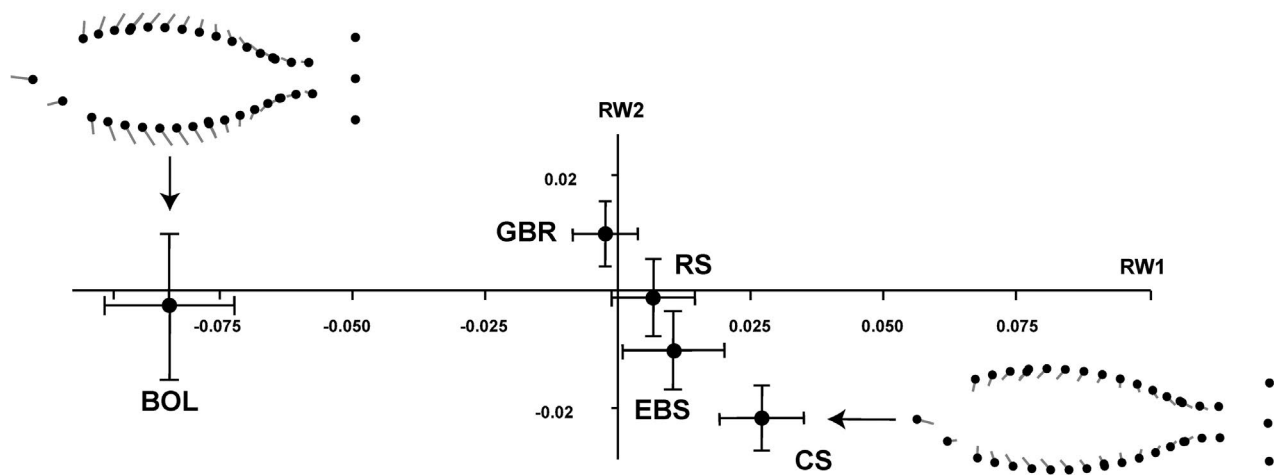


Fig. 3 - Overall group centroids of each assemblage with standard error bars. The left and right figures are on the extreme centroids (Bolca and Caribbean Sea respectively). Deformation from the consensus shape (dots) is visualized through the vectors (lines). BOL = Bolca, GBR = Great Barrier Reef, EBS = East Brazil Shelf, CS = Caribbean Sea, RS = Red Sea.

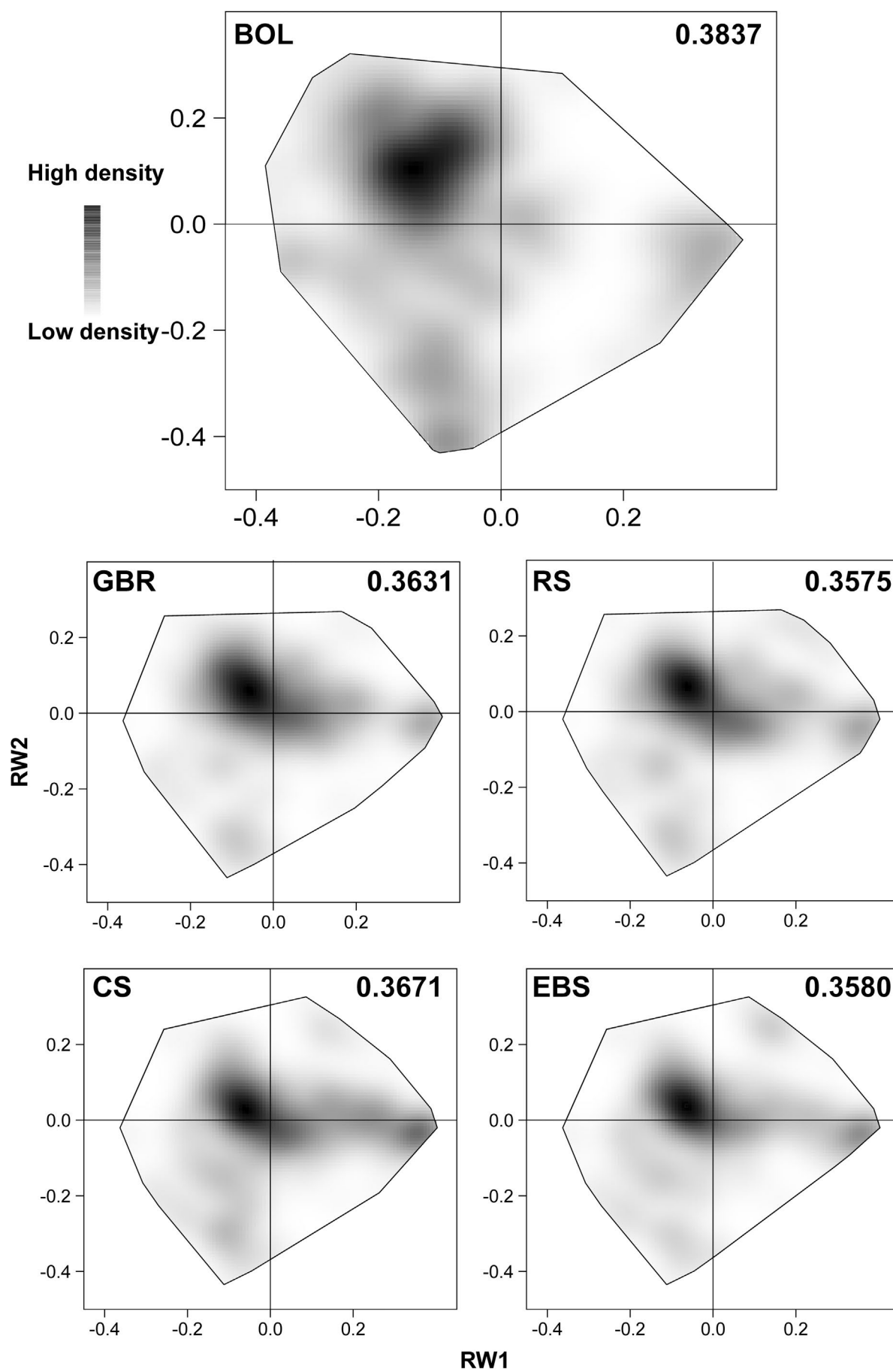
Indeed, the Bolca centroid is significantly separated from those of the Recent assemblages (Fig. 3) documenting the relative abundance of deep-bodied fishes and, therefore, a shift of the mean shape toward more elongate body from the Eocene to the Recent. The centroid of extant fish assemblages is instead closer to the consensus shape or lies on positive scores of RW1. The ANOSIM shows that convex hulls appear significantly overlapped in the morphospace ($R = 0.0461$; $p = 0.0001$), suggesting a relative stasis in terms of morphospace occupation.

In all ecosystems, the center of each morphospace built on the first two RW axes (Fig. 1) is mainly occupied by “perciforms” and some tetraodontiforms (balistids and monacanthids) that provide a low contribution to the morphological variation, being close to the consensus shape. Conversely, the extreme shapes are defined by taxa with slender body and long dorsal and anal fins (e.g., anguilliforms and ophidiiforms), elongate shape and short median fins (e.g., syngnathiforms and beloniforms), deep body and short median fins (e.g., tetraodontiforms), deep body and long median fins (e.g., pleuronectiforms and some “perciforms”). Instead, the position of the different lineages within the convex hulls built on third and fourth RWs (Fig. 2) is more difficult to interpret because there is strong overlap based on their shape. Moreover, taxa belonging to the same clade (e.g., syngnathiforms) may lie on the opposite sides of morphospace.

Based on the morphospace built on the first two RW axes, the Bolca assemblage shows the broadest area (Fig. 4; Tab. 1) due primarily to a slight excursion of the convex hull into extreme negative values on RW1 and extreme positive scores on RW2, reflecting the presence of some deep bodied “perciforms” (*Eoplatax*, *Ceratoichthys*, *Eoantigonia*, *Sorbiniperca*, *Sorbinicapros*) and some tetraodontiforms (*Eoplectus*, *Eolactoria*, *Proaracana*). This region remains unoccupied in modern fish assemblages. Based on morphospace built on the third and fourth RW axes, the Bolca area is instead the smallest due primarily to a constriction of the convex hull (Fig. 5; Tab. 1).

Nearest neighbor analysis (Tab. 1) shows that the taxa appear significantly clustered in all ecosystems ($0 < R < 1$; $p < 0.05$); this suggests no over-dispersion and no random morphospace occupation, except for the Bolca morphospace built on the third and fourth RW axes ($R \sim 1$; $p > 0.05$). The spatial distribution of the taxa, visualized through Kernel-density plots built on the first two RW axes (Fig. 4), is consistent in all the morphospaces, with the central region showing the highest intensity that corresponds to the aggregation center for those morphologies around the consensus shape (e.g., most of the “perciforms”). Other aggregation centers are located in the periphery of the morphospace, coinciding with the extreme body shapes (e.g., anguilliforms, syngnathiforms, tetraodontiforms and pleuronectiforms). The Kernel-density plot of the Bolca assemblage shows a high density of taxa in the region of the space characterized by deep-bodied morphologies compared to the Recent assemblages. Distribution of modern taxa seems to follow a biogeographic gradient because the two Indo-Pacific assemblages (Great Barrier Reef and Red Sea) show a similar patterning, as well as do those of the Western Atlantic ecosystems (Eastern Brazilian Shelf and Caribbean Sea). Although these similarities might reflect a common history (see Hodge et al., 2014) and the distribution of taxa seems to be independent by the presence of coral reef systems, the distribution of taxa of the Indo-Pacific assemblages is more concentrated towards the region of the morphospace characterized by deep bodied morphologies than in the Western Atlantic assemblages. The Bolca Kernel-density plot built on the third and fourth RW axes (Fig. 5) shows that the aggregation center is broad, suggesting a more uniform distribution of taxa in the morphospace.

The degree of morphological variation between the Recent and Bolca fish assemblages is more evident considering disparity (Fig. 6; Tab. 1). Based on the observed values, it is possible to demonstrate that: a) the Eocene assemblage has the highest observed value of morphological disparity, significantly different from that



	Area		Patterning (R values)		Morphological disparity		
	RWs 1-2	RWs 3-4	RWs 1-2	RWs 3-4	Observed	95% lower CI	95% upper CI
BOL	0.3837	0.1566	0.8904*	0.9477	0.0872	0.0779	0.0955
GBR	0.3631	0.1875	0.7979*	0.8043*	0.0600	0.0550	0.0647
RS	0.3575	0.1935	0.8117*	0.8486*	0.0641	0.0593	0.0691
CS	0.3671	0.1970	0.8111*	0.8070*	0.0675	0.0625	0.0727
EBS	0.3580	0.1680	0.7920*	0.8875*	0.0678	0.0617	0.0735

Tab. 1 - Main patterns of morphospace occupation and morphological diversity. The values of area and patterning are from Nearest neighbor analysis. Disparity was calculated as sum of variances. The asterisks indicate significant aggregation of the points ($p < 0.05$). BOL = Bolca; GBR = Great Barrier Reef; RS = Red Sea; EBS = East Brazil Shelf; CS = Caribbean Sea.

of Recent assemblages; b) Western Atlantic ecosystems have similar morphological disparity values, with a mean value higher than those of the Indo-Pacific; c) the Great Barrier Reef has the lowest observed disparity value. However, although the difference in disparity between Eocene and Recent assemblages is clearly significant (Bolca lower 95% CI \gg all extant upper 95% CI disparity), the differences among Recent assemblages should be interpreted cautiously because of the similar large confidence intervals.

DISCUSSION

Comparative analysis of morphospace between Eocene and modern shallow marine fish ecosystems revealed no significant differences between Bolca and Recent fish assemblages in terms of area and overlap, thereby suggesting a substantial stasis in terms of morphospace occupation. Nevertheless, the different position of group centroids revealed that elongation of the body represents part of the shape variation between Bolca and Recent fish communities. Elongation, as dominant axis of body shape evolution of modern tropical shallow marine fishes, has been demonstrated by Claverie & Wainwright (2014), who suggested that changes in body elongation are primarily related to adaptive solutions to environmental changes. Therefore, it is possible to show the existence of a general trend documenting an elongation of the mean shape since the Eocene, suggesting that such a trend should be regarded from an historical perspective.

The patterning, visualized through Kernel-density plots, also reveals a substantial similarity between the Recent ecosystems pertaining to the same marine realm, reflecting a biogeographical separation of the Indo-Pacific and Western Atlantic areas (Kulbicki et al., 2013; Hodge et al., 2014). On the other hand, although the highly diverse Indo-Pacific region is regarded as one of the most diversified marine hotspots, it is characterized by a lower morphological disparity compared to the Bolca ecosystems. The Great Barrier Reef and Red Sea contain a high number of species with morphologies close to the center of morphospace due, at least in part, to the more

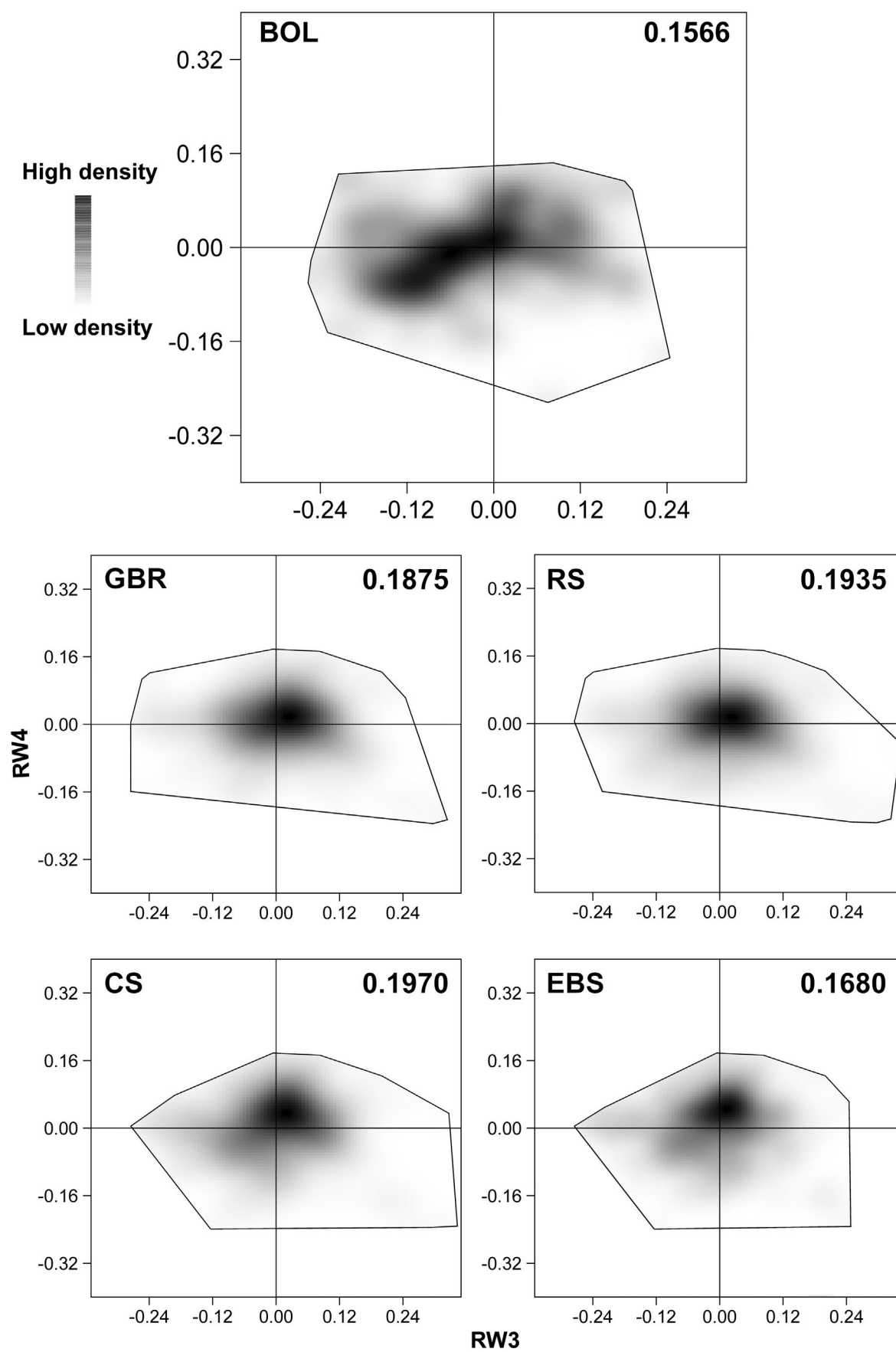
conservative history of the Indo-Pacific with respect to the Western Atlantic realm (e.g., Bellwood & Wainwright, 2002).

Although in modern fish assemblages the presence of many genera with similar morphologies could potentially result in a lower disparity with respect to that of the Bolca fish assemblage, this would not explain the greater range of morphologies of Bolca fishes, which are due in large part to the remarkable increase of disparity of spiny-rayed acanthomorph fishes that took place in the early Paleogene (Friedman, 2010). Fossil and molecular evidences concur to show that most of the representatives of modern reef fish lineages appeared after the end-Cretaceous mass extinction (see Price et al., 2014); consequently, it is reasonable to suggest that the high disparity exhibited by the Bolca assemblage mainly represents the product of the early diversification of forms that originated to replace the victims of extinction.

The remarkable morphological richness of the Bolca assemblage and the morphological similarity of certain Eocene fishes with extant reef-associated taxa were traditionally explained with the possible presence of a coral reef (Choat & Bellwood, 1991; Bellwood, 1996) in the area surrounding the depositional environment. Although it is commonly assumed that coral reefs were present in the Bolca area, sedimentological and paleontological evidences supporting this hypothesis are sparse (e.g., Landini & Sorbini, 1996; Zamagni et al., 2012; Papazzoni et al., 2014). Moreover, Bellwood (1997) demonstrated that the Bolca fish fauna exhibits most taxonomic similarities with modern temperate and subtropical marine ecosystems not associated with coral reefs.

Several studies have been focused on the potential role of coral reefs as drivers of fish diversification (e.g., Bellwood & Wainwright, 2002; Alfaro et al., 2007; Cowman & Bellwood, 2011; Frédérick et al., 2013; Sorenson et al., 2014). However, the remarkable morphological richness and disparity of Bolca, which are decoupled with the paleontological evidence of the presence of a developed coral reef system, are not consistent with the results of these studies. Moreover, the early Paleogene decline of coral reefs suggests that these should not be considered as the main driving force

Fig. 4 - Morphospace occupation visualized through Kernel-density plots built on the first two RW axes, showing the distribution and density of taxa on morphospaces. The values close to the abbreviation of each ecosystem indicate the area of the convex hulls. BOL = Bolca; GBR = Great Barrier Reef; RS = Red Sea; CS = Caribbean Sea; EBS = East Brazil Shelf.



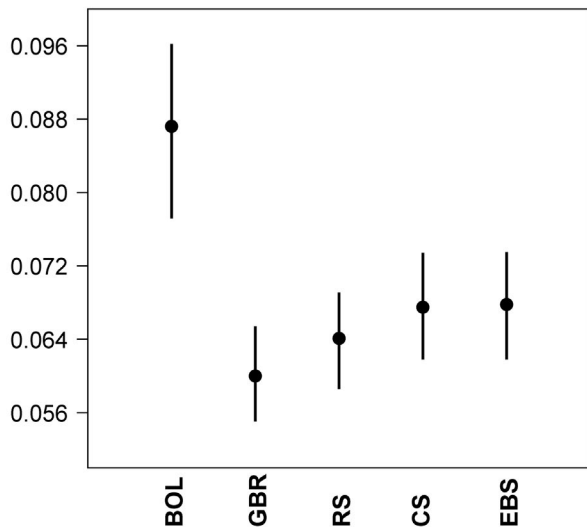


Fig. 6 - Graphic representation of morphological disparity based on data summarized in Tab. 1. Dots represent the observed values of disparity, lines represent the 95% confidence interval after bootstrap procedure. BOL = Bolca, GBR = Great Barrier Reef, RS = Red Sea, CS = Caribbean Sea, EBS = East Brazil Shelf.

promoting the morphological richness observed at Bolca. Price et al. (2014) suggested that Cenozoic reefs were colonized after the evolutionary diversification of the spiny-rayed fish lineages, while some authors (Bellwood, 2003; Bellwood et al., 2014a, b, 2015) argued that the fossil record supports the hypothesis that the early Eocene coral reefs may have promoted the exploitation of new ecological resources as demonstrated by the development and expansion of piscine herbivory, high precision benthic feeding, and nocturnal feeding (Goatley et al., 2010; Schmitz & Wainwright, 2011; Bellwood et al., 2014a). Our results appear to be consistent with the hypothesis that coral reefs acted “as a sanctuary”, which may have adopted the fish lineages associated with modern reefs from a preexisting non-reef fauna, representing a cradle for the maintenance of diversity and without a substantial specific role in the origin and evolution of the morphological richness (Bellwood & Wainwright, 2002). Such a hypothesis appears to be supported by paleontological and molecular evidence that indicate that the earliest stages of the evolutionary history of several groups of modern reef fishes including acanthuroids, ephippids, chaetodontids, labrids, pomacanthids and holocentrids were not closely linked to coral reefs (see Bellwood & Wainwright, 2002). Modern coral reef fish assemblages likely developed during the Oligocene and Miocene, coincident with a global expansion of carbonate platforms, an increase of the ecological importance of *Acropora* in reef systems, and a rapid cladogenesis of major reef groups (Cowman et al., 2009; Cowman & Bellwood, 2013; Bellwood et al., 2014a).

It is interesting to note that our results concur to suggest that a likely marine non-reef fish fauna during a ‘greenhouse’ interval did not exhibit a significantly different morphospace occupation than the coral reef systems during the modern ‘icehouse’ climatic interval. Such a stasis more likely represents the result of the rapid niche-filling and morphospace saturation that took place within the first million years after the end-Cretaceous extinction (Near et al., 2013; Price et al., 2014, 2015). This is particularly evident for spiny-rayed fishes that exploited the extinction event by producing a wide range of morphologies and body plans to explore the vacant ecological resources (Friedman, 2009, 2010). Such a scenario stands in sharp contrast to the patterns observed in other vertebrate groups (e.g., mammals), which were affected by major changes of morphological diversity during the Cenozoic (see, e.g., Webb & Opdyke, 1995; Figueirido et al., 2012).

The end-Cretaceous extinction has dramatically reset the marine system in favor of different lineages of teleost fishes, acting as a major driver in the extraordinary rise of this group of vertebrates in both shallow waters and open oceanic settings (see also Sibert & Norris, 2015). Finally, the vast early Paleogene diversification of teleost lineages is also positively correlated with a progressive rise of the sea level stand and sea temperatures that culminated about 50 Ma (see Zachos et al., 2001), approximately in coincidence with the deposition of the fossiliferous strata of Bolca.

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Fig. 5 - Morphospace occupation visualized through Kernel-density plots built on the RW3 and RW4, showing the distribution and density of taxa on morphospaces. The values close to the abbreviation of each ecosystem indicate the area of the convex hulls. BOL = Bolca; GBR = Great Barrier Reef; RS = Red Sea; CS = Caribbean Sea; EBS = East Brazil Shelf.

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