Morphological evolution in the deep blue sea

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While coral reefs are known to harbour an astonishing and extensive diversity of species, few studies have been performed on the role of the pelagic environment - or, in other words, the deep blue sea - in species diversification. However, a recent study by the University of Liège has shown that this pelagic environment and other associated environments can lead to a greater diversity of shapes in some groups of fishes, compared with reef environments.

**Speciation** is a complex and fascinating phenomenon, and a breeding ground for many scientific publications. Its complexity can be explained by the fact that numerous factors, both intrinsic (genetic diversity, morphology, etc.) and extrinsic (new **ecological niche**, competition, predation, etc.), may be responsible for diversification processes.

In the marine realm, it has been proved that tropical coral reefs were (and are) a driver for diversification among several fish **clades**. This complex and highly productive habitat offers many possibilities for diversification, both from a morphological point of view (i.e. disparity) and in terms of species (speciation). For many marine fish families, different studies have thus identified greater diversity in reef environments than in non-reef environments.
Life outside the reefs

Bruno Frédérick, from the Laboratory of Oceanology at the University of Liège, and his colleagues from the universities of Turin and Pisa, decided to go against these findings: what about the role of non-reef environments, such as the pelagic environment (in the open sea, more poetically known as the 'deep blue sea'), or sandy areas close to the coast, in the evolution of species?

"The idea behind this paper (1) is to demonstrate the opposite of what is generally accepted concerning reef environments", explains Bruno Frédérick, the main author of the study. "We started out from the hypothesis that it is actually the pelagic marine environment, i.e. the 'deep blue sea', or even shallower environments albeit associated with sandy areas, that can be conducive to diversification".

And to test the hypothesis? A fish clade. One that must have a sufficiently large number of species, including enough fossils, in order to be able to follow the evolution of their diversification, and the possibility of finding species associated with reef and non-reef species. The winner? The group of carangoid fishes, i.e. teleost fishes such as jacks or remoras with suckers, known for their phoretic association with sharks and other large fish.

Databases made available by scientists worldwide

It was essential to obtain morphological and molecular data for the study in order to apply a timescale to this clade's diversification. This data was collected from public databases and museums.

"The current trend in the scientific world is to make data accessible to everyone, especially through websites such as Morphobank, or sites offering genetic data, in particular PubMed."
Example of images that were used for the morphological study of Carangoid fishes. *Trachinotus blochii* top left, *Carangoides chrysophrys* top right and *Exheneis* sp. below.
“My colleague Francesco Santini [from Pisa] visited natural history museums to take pictures of the species that interested us. It’s something that’s coming back in the study of biodiversity. Five, ten years ago, we saw museums as a place where organisms were put in alcohol and forgotten on the shelf. But that’s no longer the case;
many researchers are returning to these museums to take photos (or other images) of organisms, in order to get them out of their jars and study their morphology. Museums provide us with access to an enormous bank of species”, Dr. Frédérick explains.

A method of collection that in no way resembles Hollywood’s adventurer image of the scientist, but one that has led to a database containing 384 specimens from 178 species of carangoid fishes, including 24 fossilised species. "We needed a group of fish that had a decent amount of well-preserved fossils, so that we could take precise morphological measurements."

Fossil of Ceratoichthys pinnatiforsem (Blainville, 1818) dating from the Eocene (late Ypresian) from Monte Bolca (Pesciara cave), left side view. ©Roberto Lazzarin (Collezione Museo Civico di Storia Naturale di Verona).

No difference in the rate of speciation...

In total, 47 landmarks were chosen to describe the body shape of the specimens in lateral view, thus capturing the body’s elongation (i.e. the ratio between the fish’s length and height) and the curvature of the cephalic region. Elongation is directly linked to swimming performance, such as manoeuvrability, acceleration and endurance, characteristics that provide an advantage in the pelagic environment. As for the curvature of the cephalic region, there are significant variations within this group, thus providing a good view of their morphological evolution.

Landmarks used to analyse variation in fish body shape, illustrated in Alepes djebada. (c) CC J.E. Randall: http://pbs.bishopmuseum.org/images/JER/.
Thanks to a combination of molecular evolution models and fossil calibration points, it was possible to produce a time-calibrated phylogeny. Genetics provided phyletic relationships and the fossils imposed time constraints. Evolution in diet (piscivorous or non-piscivorous) and type of habitat (reef or non-reef associated) was reconstituted on this tree. For extinct species, the habitat was deduced from the rocks where the fossils were found.
Summary of the ecological (diet and habitat) histories on the consensus timetree of carangoid fishes using stochastic mapping. We can see here that it isn’t possible to fully ascertain whether the common ancestor lived in a reef or non-reef habitat (50/50).

"In our analyses, we divided the type of biodiversity into two different blocks: the number of species and disparity, which corresponds to morphological diversity. Hence, there are two types of diversity that are explored differently. With time-calibrated phylogeny, the length of the branches express the time lapse between the divergence of two lineages. With the information regarding time, we can calculate the rate of speciation. And in our case, we didn’t observe any differences in the rate of speciation, regardless of whether the species is a reef-dweller or not."

...but an effect on disparity

However, as regards disparity, analyses of morphospaces reveal something completely different, as Bruno Frédéric explains: "There is greater diversity in shape in the current non-reef environment than several million years ago. Therefore, the calculations regarding shape disparity levels coincide with the calculations..."
concerning rate of morphological evolution: this shows that 50 million years ago, there was clearly less morphological diversity in the non-reef environment compared with today."

> Level of disparity according to the periods and habitats, through two methods of calculation, (a) and (b). The two graphs show that disparity is currently greater in the non-reef environment than during the Eocene.

"This shows that the non-reef environment clearly had an impact on the diversification of these fishes. If we use phylogeny to do the calculation, there is strong support for a model with two rates of morphological diversification: the rate of morphological evolution among non-reef dwellers was nearly twice as much compared with reef-dwelling species."

**Ecological niches left vacant**

It is necessary to be able to swim fast, over long distances and be a master of camouflage in pelagic environment, which offer very little physical shelter. Elongated bodies and scales reflecting the light are therefore major advantages in terms of survival. "Several types of shape appeared, which are a compromise between travelling over long distances, at high speed, and optimising camouflage."

Hence the study's conclusions on the factors that may have led to this diversification: "Our hypothesis is that since many species have disappeared from the pelagic environments, the Carangoid fishes were able to sweep into the available space and occupy the niches that had become available. But as to why it was these fish that explored this environment, that's another question to which I don't yet have an answer. However, we do show that the pelagic environment was a factor of diversification for this group of fish."

An important discovery because up until now, very few studies have been able to prove that the pelagic environment could also lead to diversification.

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(1) Non-reef environments impact the diversification of extant jacks, remoras and allies (Carangoidei, Percomorpha), Frédéric Bruno et al. Proceedings of the Royal Society B : Biological Sciences, nov. 2016.